Biolocomotion without inertia

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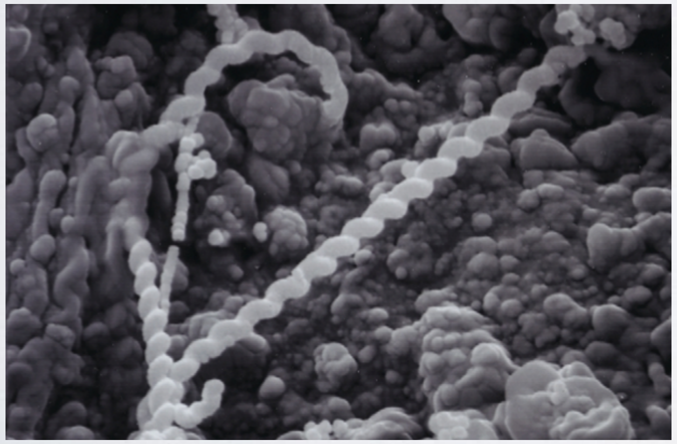
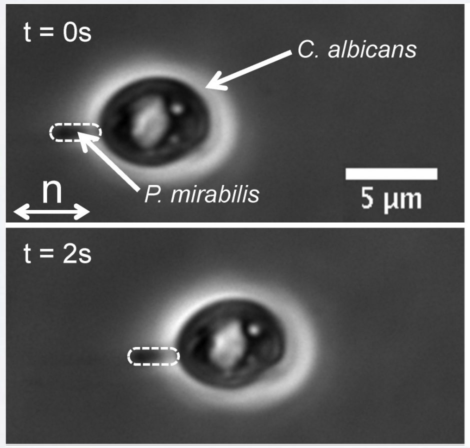
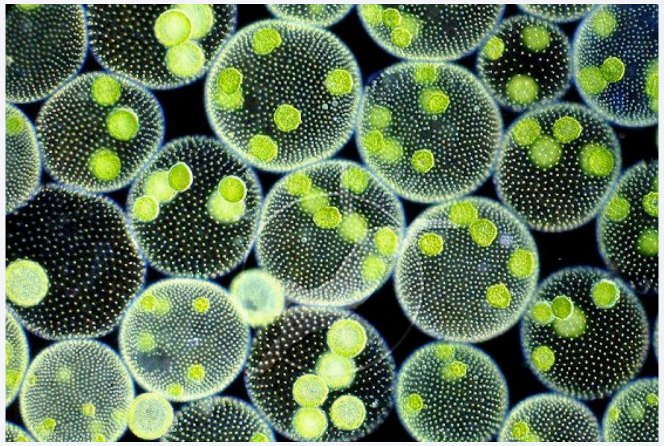
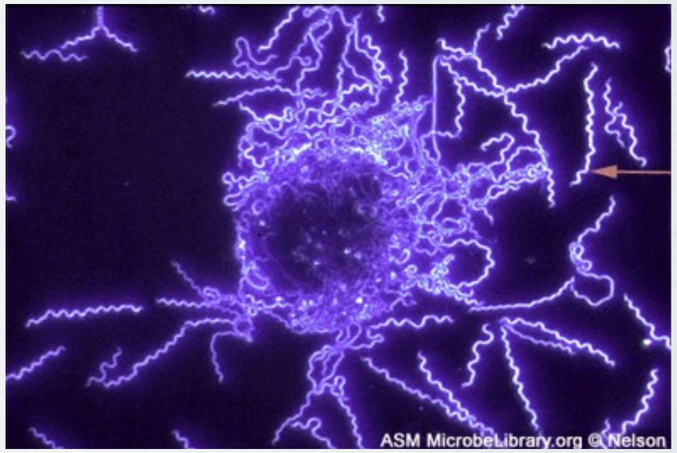
ShelleyFest 2019, Ann Arbor, MI
Tutorial Session

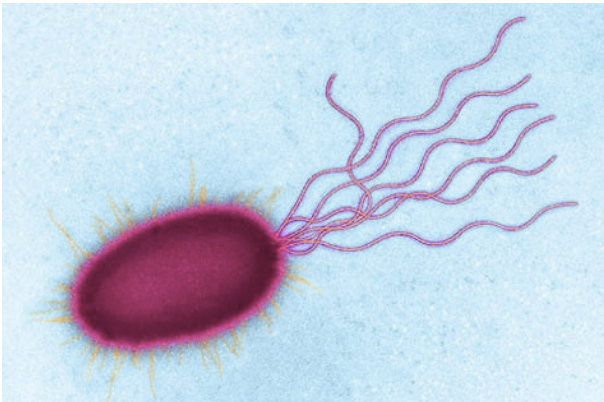




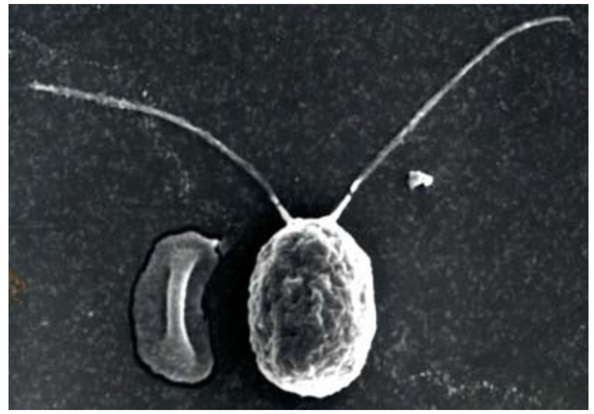




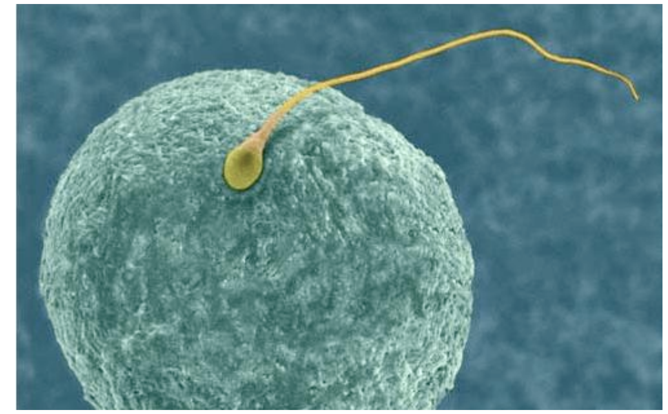
Evolution of swimming strategies: Scale Matters.



Escherichia coli
D. Kunkel Microscopy

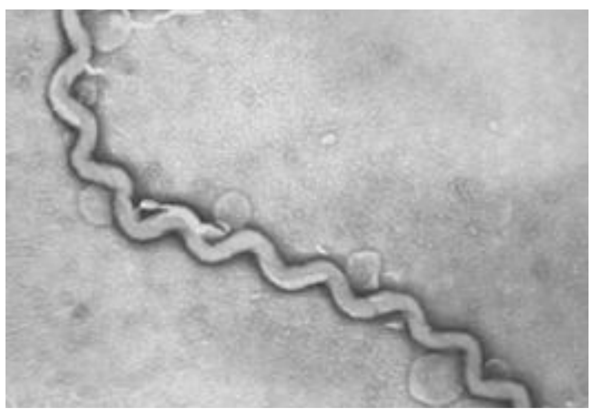


Chlamydomonas
D. Howard, UWLC

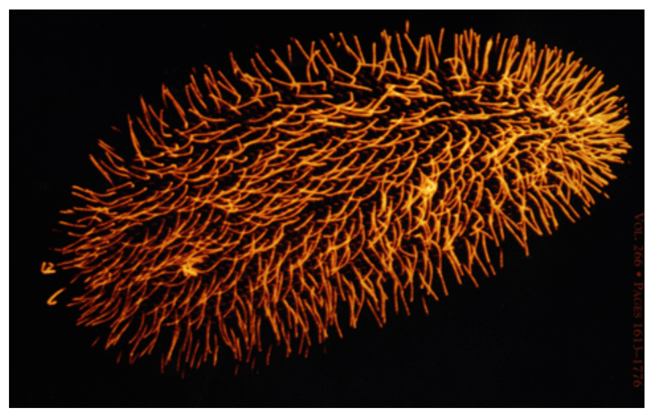


Human spermatozoa
D. Kunkel Microscopy

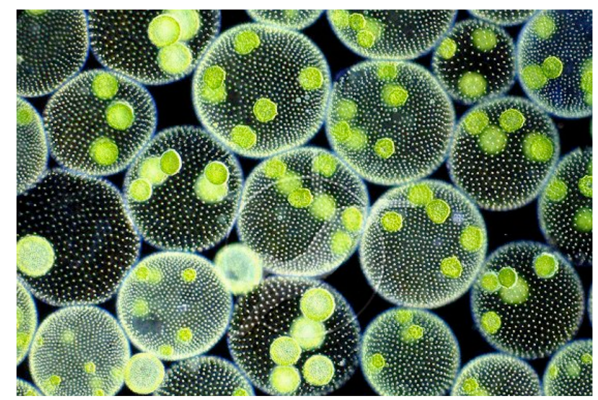
Tracheal epithelium
D. Kunkel Microscopy



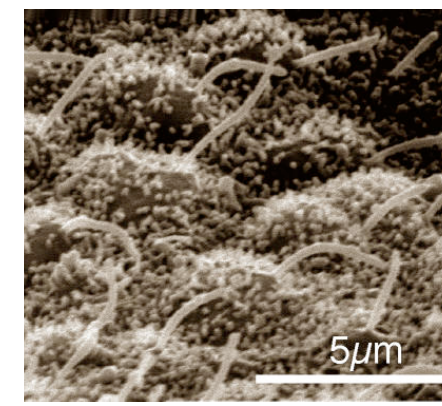
Spirochete
W. Ellis, U. Belfast



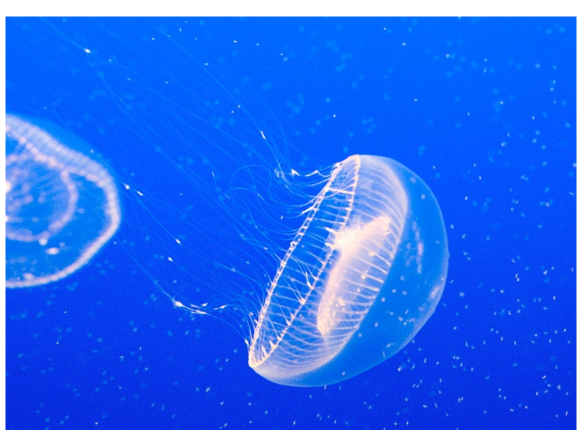
Paramecium
A. Fleury, Orsay



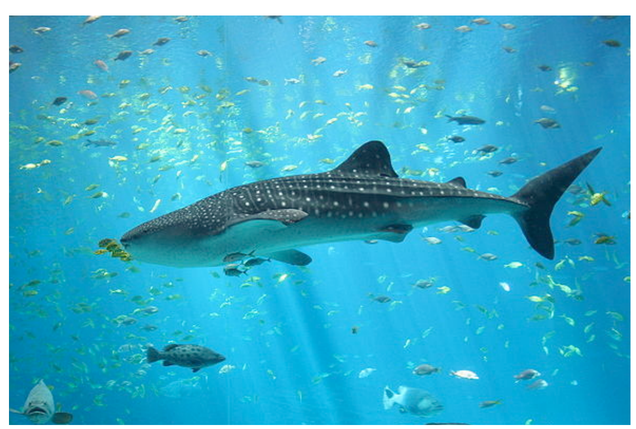
Volvox
Warren Photography



Mouse embryo nodal cilia
S. Nonaka, NIBC, Japan



Crystal Jellyfish
Wikimedia commons

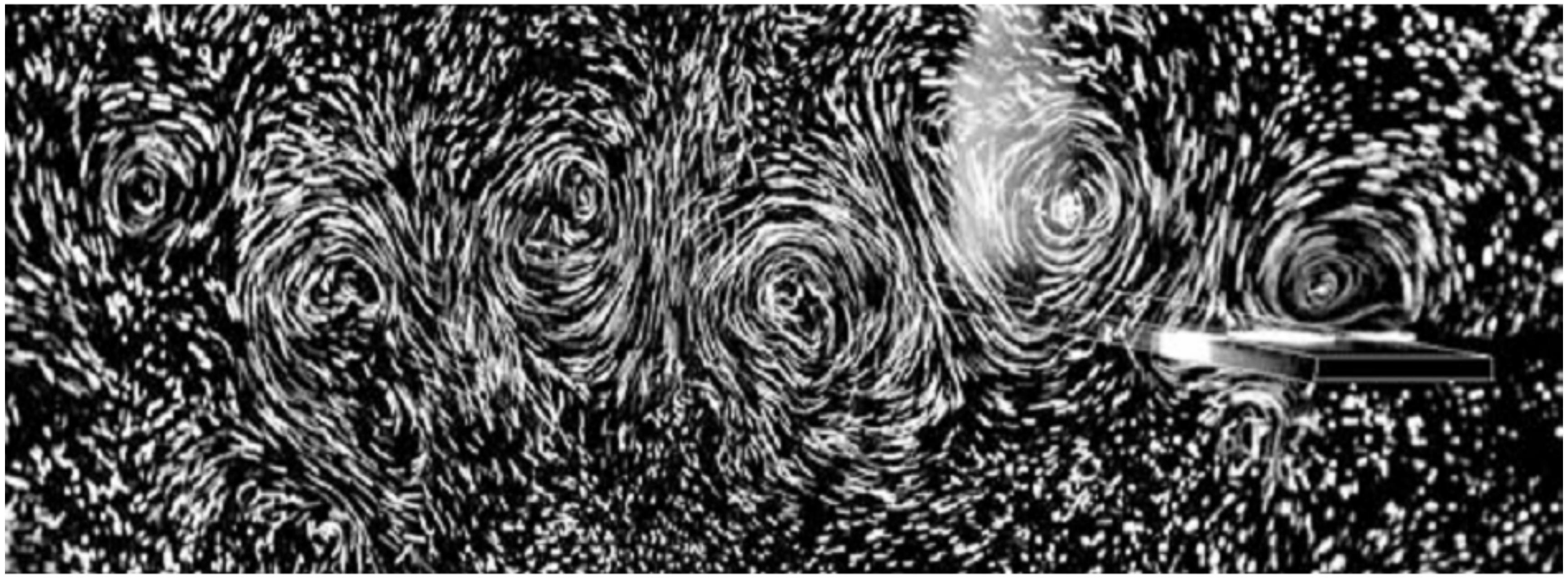


Whale shark
Georgia Aquarium

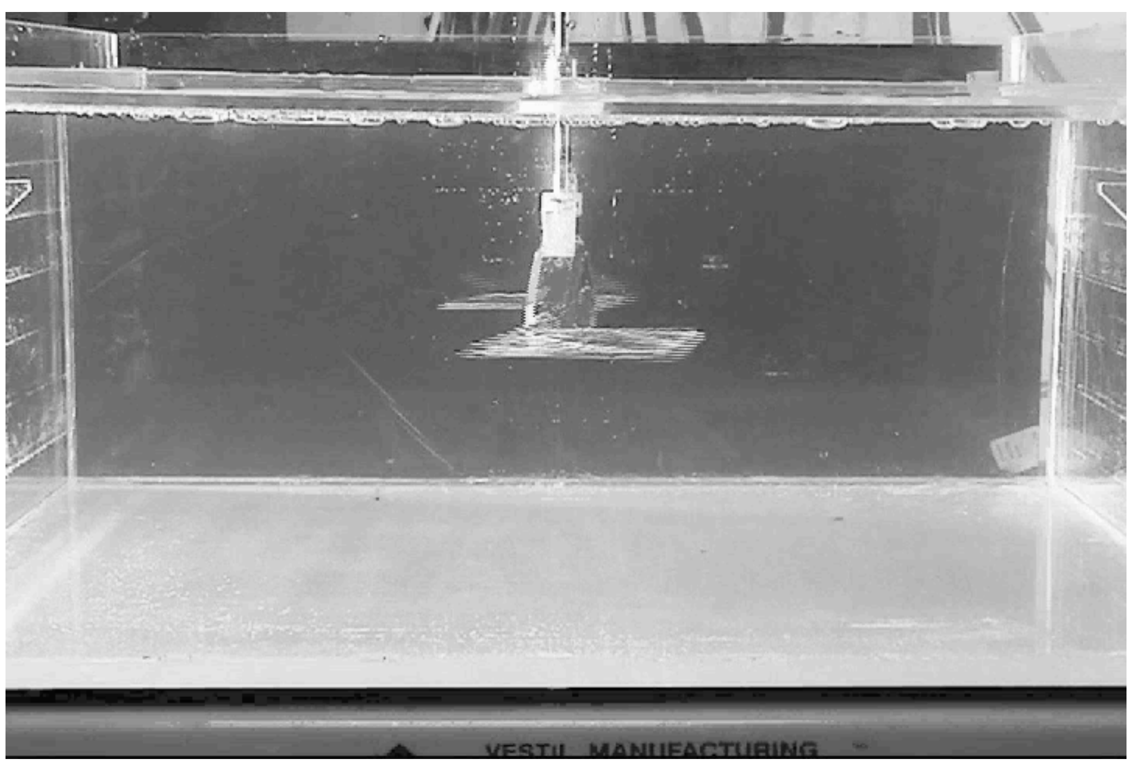
Dragonfly
Wikimedia commons

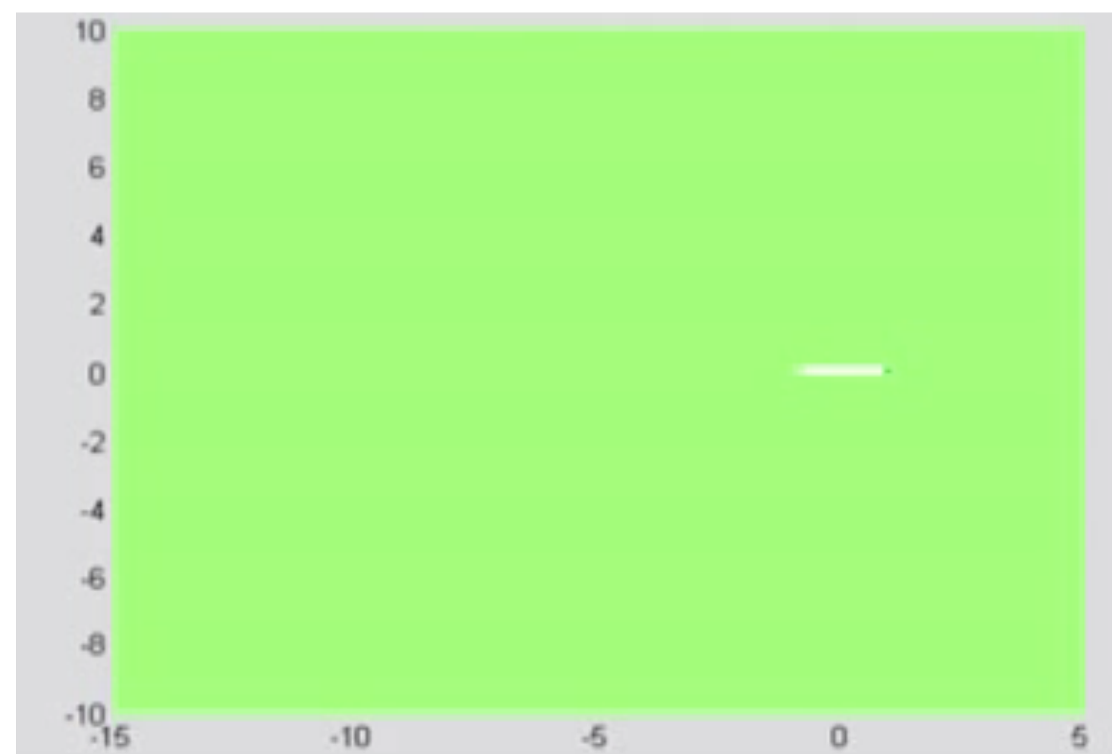
Barn Owl
Ron Dudley

How do ***you*** swim?



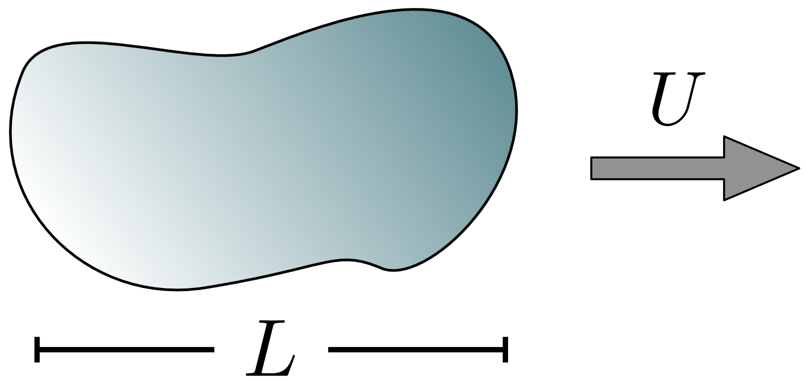
Vandenberghe, Zhang, & Childress (2004).





Alben & Shelley, *PNAS*, 2005
Spagnolie, Moret, Shelley, & Zhang, *Phys. Fluids*, 2010
Ristroph & Childress, *J. Roy. Soc. Interface*, 2014

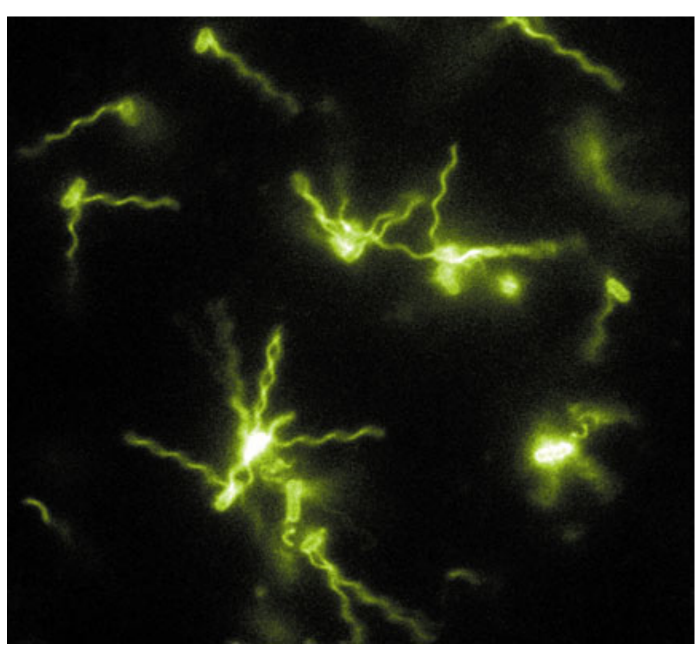
Dynamic similarity: the Reynolds number

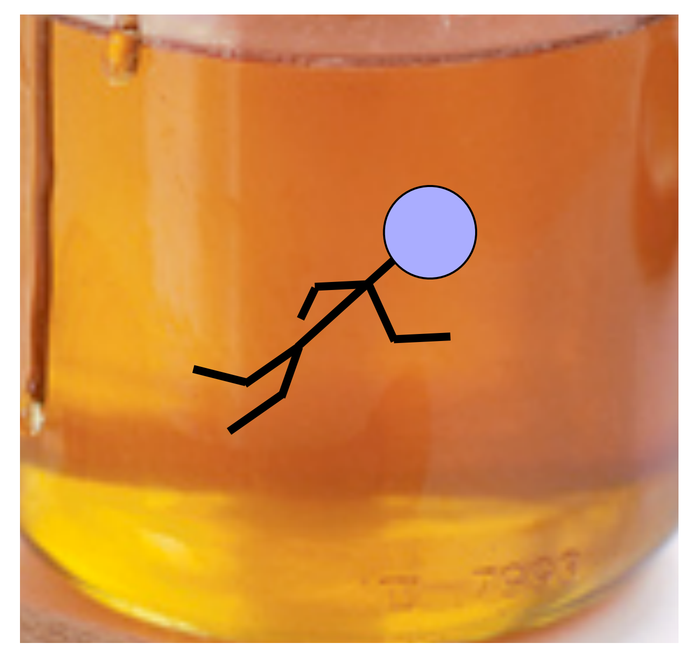


$$\mathrm{Re}\,(\mathbf{u}_t + \mathbf{u}\cdot\nabla\mathbf{u}) = -\nabla p + \nabla^2\mathbf{u}$$

$$\nabla\cdot\mathbf{u} = 0$$

$$\mathrm{Re} = \frac{\rho U L}{\mu} \quad \left(\frac{\text{inertial effects}}{\text{viscous effects}}\right)$$



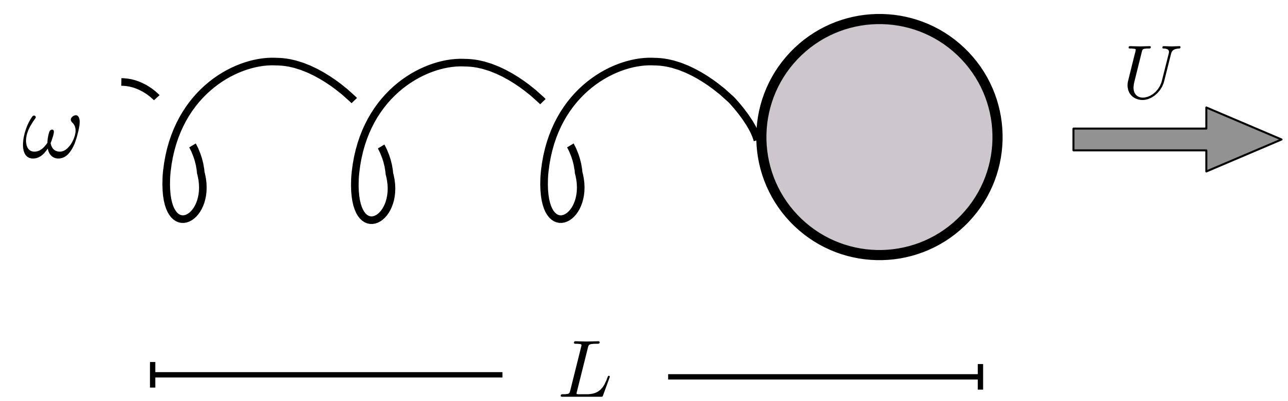


Real numbers

$$\mathrm{Re}\,(\mathrm{St}\,\mathbf{u}_t + \mathbf{u}\cdot\nabla\mathbf{u}) = -\nabla p + \nabla^2\mathbf{u}$$

$$\mathrm{Re} = \frac{\rho U L}{\mu} \qquad \mathrm{St} = \frac{L\,\omega}{U}$$

Reynolds number Strouhal number



	L	U	ω [Hz]	St	Re
Bacteria	1 μm	10 μm/s	100	10-100	10^{-5}-10^{-4}
Paramecium	100 μm	1 mm/s	10	1	10^{-1}
Wasp	1 mm	1 mm/s	400	0.25	15
Fish	50 cm	1 m/s	1	1	10^4-10^5

(Childress, 1980)

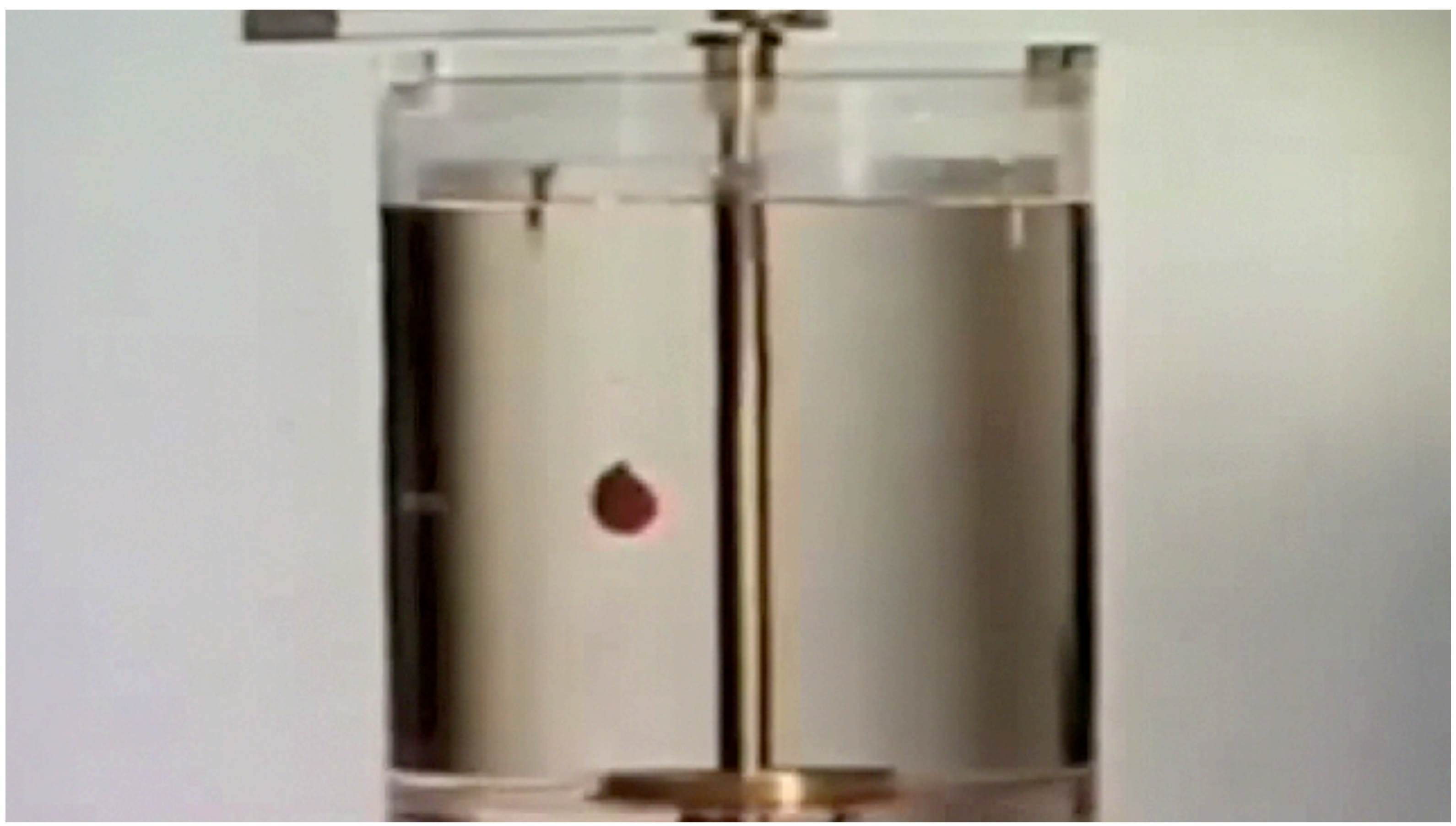
At **zero** Reynolds number there is **no** inertia, and time is merely a parameter.

Stokes equations:

$$\cancelto{0}{\mathrm{Re}\,(\mathbf{u}_t + \mathbf{u}\cdot\nabla\mathbf{u})} = -\nabla p + \nabla^2\mathbf{u}$$

$$\nabla\cdot\mathbf{u} = 0$$

Linearity + time-independence of the Stokes equations = kinematic reversibility:
An instantaneous reversal of the forcing does not modify the flow patterns, only the direction in which they are occurring.



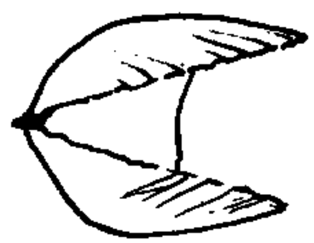
Silicone oil
Speed: x4

G.I. Taylor
National Committee for Fluid Mechanics Films, 1961

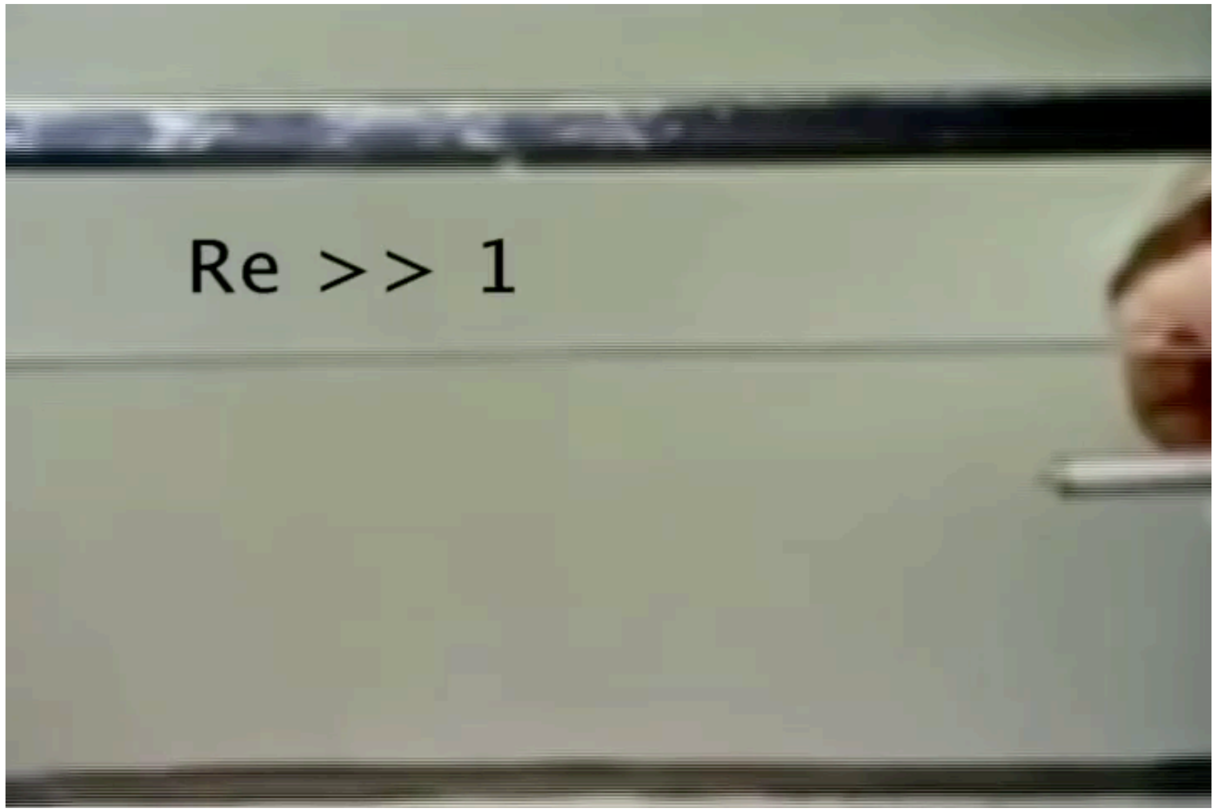
Swimming strategies must respect fluid mechanics!

The Scallop Theorem

Life at Low Reynolds Number,
E. M. Purcell, 1977

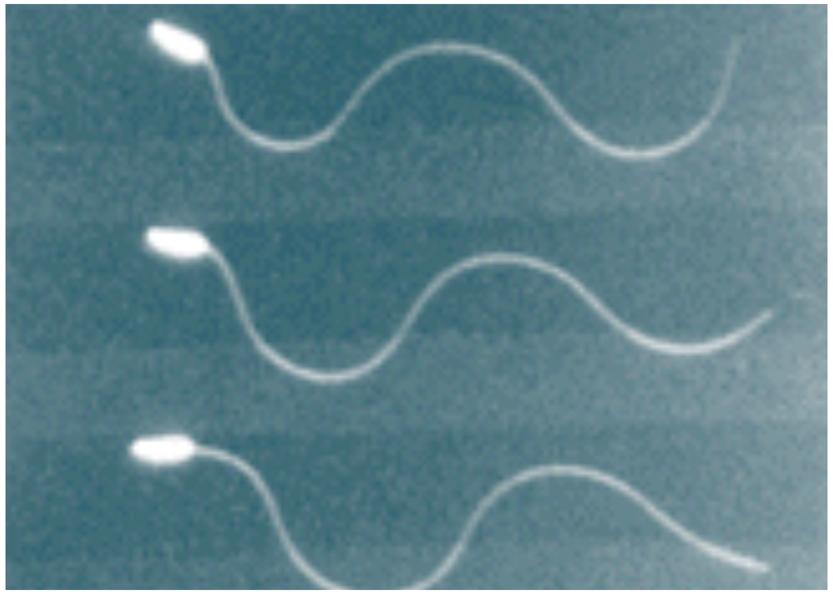


G.I. Taylor (NCFMF)



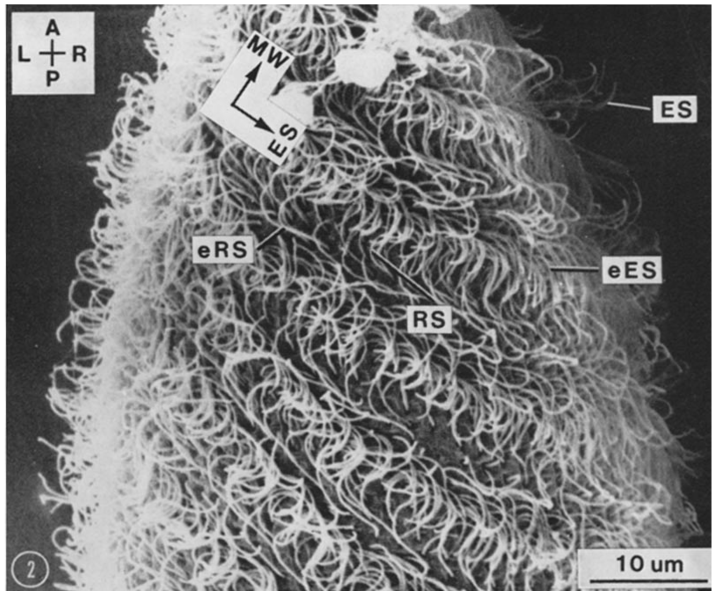
Microorganisms **must** use different strategies to swim... and they do.

Spermatozoa



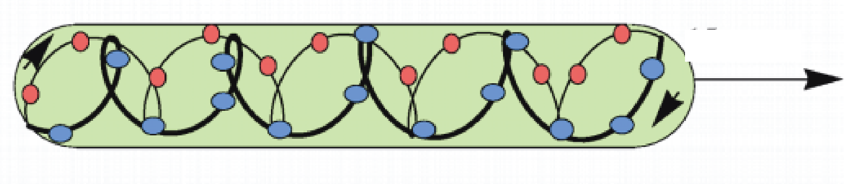
C.J. Brokaw, Caltech

Paramecia



Tamm, *J. Cell Biol.*, 1972

Synechococcus



Nan et al., *Curr. Biol.* 2014

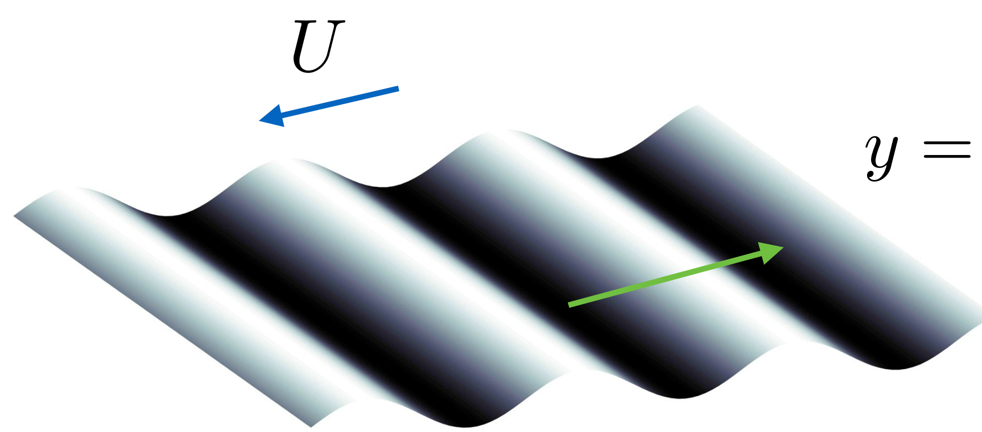
Life at intermediate Reynolds number is *amazing*!

2 cm

Shell-less pteropod mollusc ***Clione antarctica***
Childress & Dudley, (J. Fluid Mech. 2004)

An early mathematical model: “Taylor’s swimming sheet” (Taylor, 1951)

$$-\nabla p + \mu \nabla^2 \mathbf{u} = \mathbf{0}$$
$$\nabla \cdot \mathbf{u} = 0$$



Define a stream-function for the velocity: $\mathbf{u} = \nabla^{\perp}\psi = (\psi_y, -\psi_x)$

$$\Rightarrow \nabla^4 \psi = 0$$

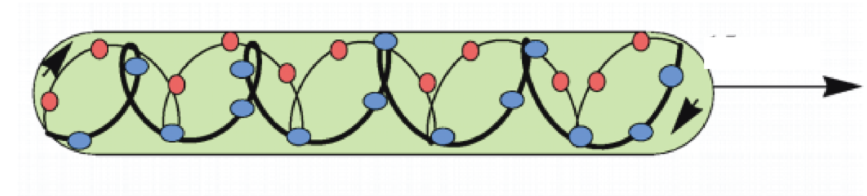
Expand about small amplitude $\varepsilon = bk \ll 1$

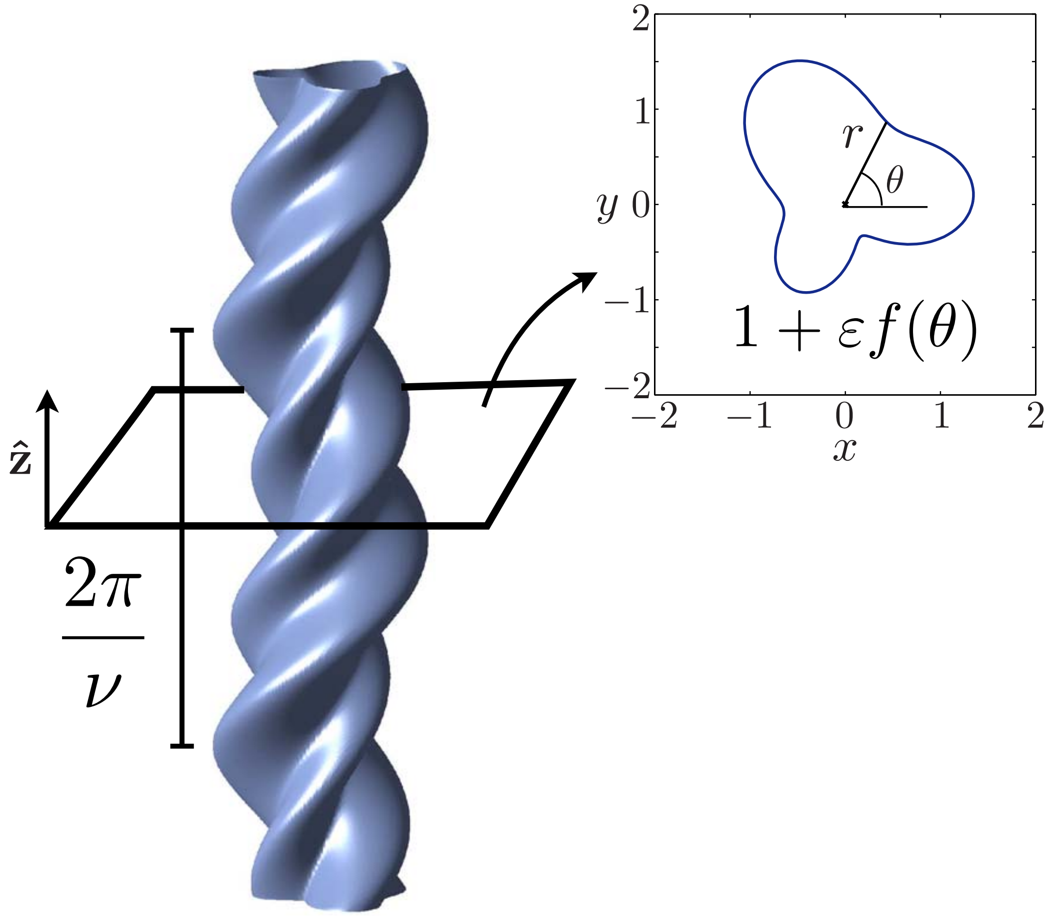
$$\Psi(x, y, t; \varepsilon) = \psi^{(0)}(x, y, t) + \varepsilon \psi^{(1)}(x, y, t) + \varepsilon^2 \psi^{(2)}(x, y, t) + ...,$$
$$U = U(\varepsilon) = U^{(0)} + \varepsilon U^{(1)} + \varepsilon^2 U^{(2)} + \cdots$$

Solve Stokes equations order by order…

$$U = \frac{1}{2}\frac{\omega}{k}\varepsilon^2 + O(\varepsilon^4) \approx \frac{1}{2}\omega k b^2$$ (Quiz: Why nothing at first order?)

Helical waves may be treated similarly via helical symmetry





$$\mathbf{x} = r\left[\cos(\nu\zeta+\theta)\hat{\mathbf{x}} + \sin(\nu\zeta+\theta)\hat{\mathbf{y}}\right] + \zeta\hat{\mathbf{z}}$$

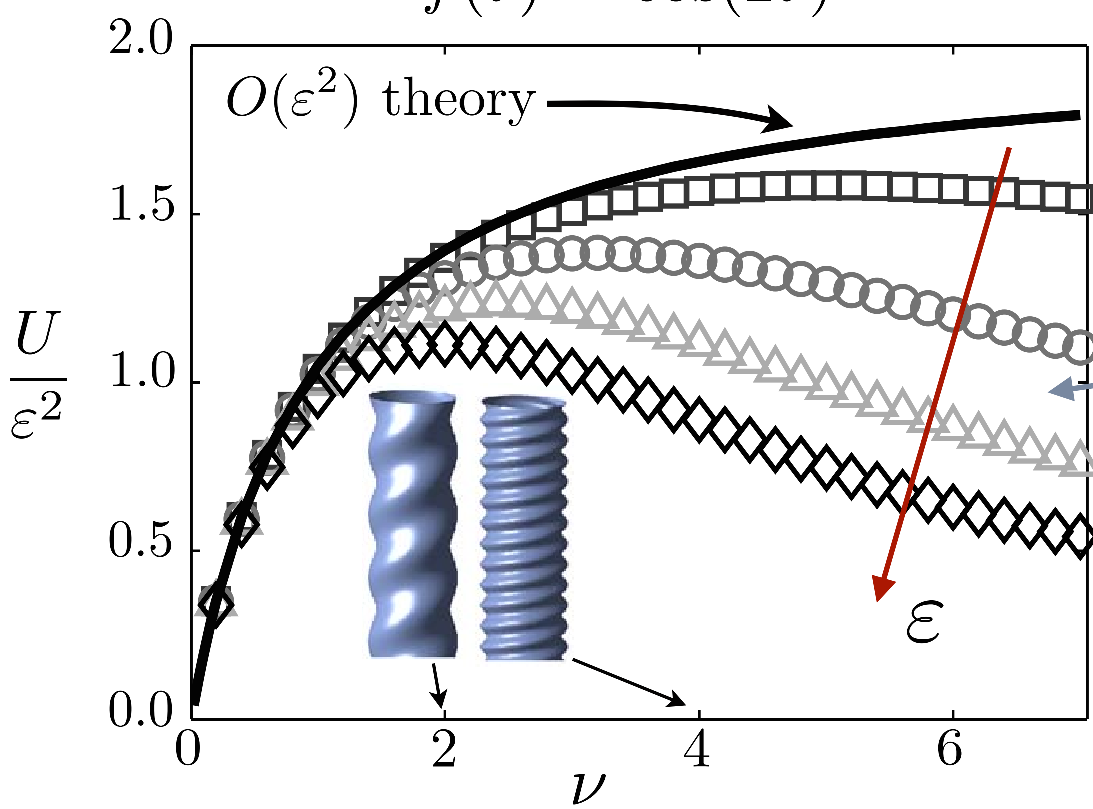
$$\mathbf{v}(r,\theta,\zeta) = u(r,\theta)\hat{\mathbf{r}} + v(r,\theta)\hat{\boldsymbol{\theta}} + w(r,\theta)\hat{\mathbf{z}}$$

$$\nabla = \hat{\mathbf{r}}\frac{\partial}{\partial r} + \hat{\boldsymbol{\theta}}\frac{1}{r}\frac{\partial}{\partial \theta} + \hat{\mathbf{z}}\left(\frac{\partial}{\partial \zeta} - \nu\frac{\partial}{\partial \theta}\right)$$

$$\cdots$$

$$U = \frac{1}{2}\frac{\omega}{\nu}\varepsilon^2\sum_{k\geq 1} J_k|\hat{f}_k|^2 + O(\varepsilon^4)$$

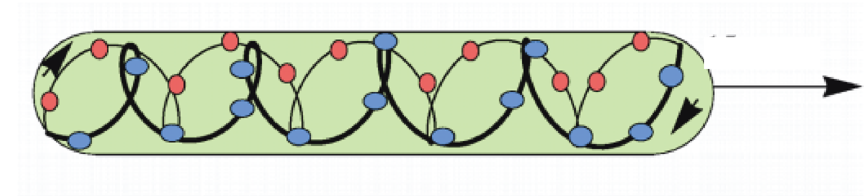
$f(\theta) = \cos(2\theta)$

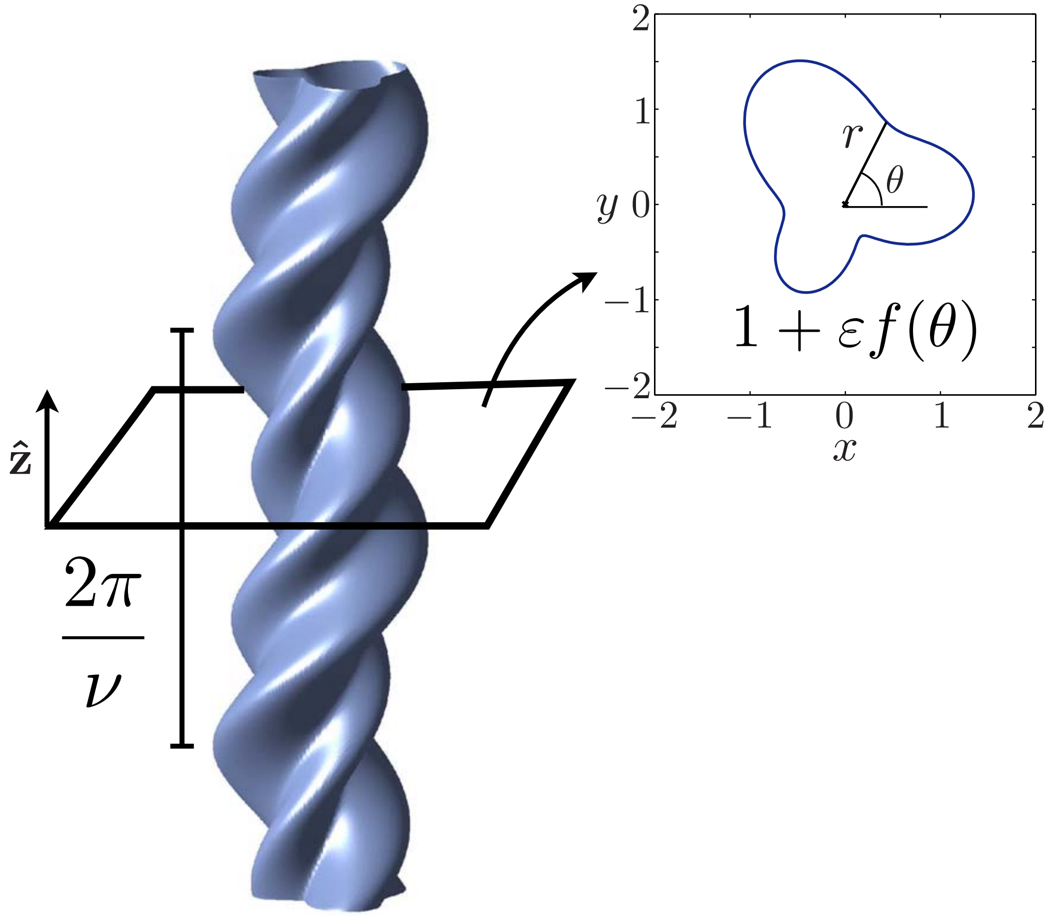


"Boundary layer" develops near the body for small helical pitch

Li & Spagnolie, *Phys. Fluids*, 2014 & 2015

Helical waves may be treated similarly via helical symmetry





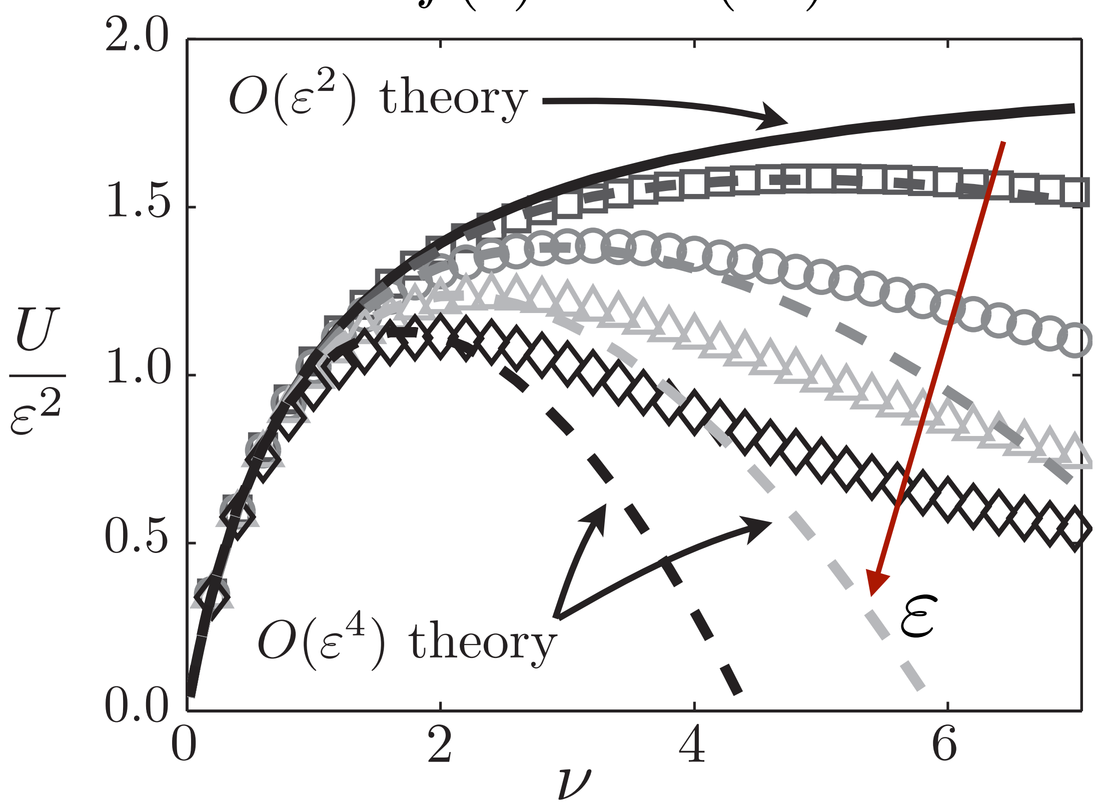
$$\mathbf{x} = r\left[\cos(\nu\zeta+\theta)\hat{\mathbf{x}} + \sin(\nu\zeta+\theta)\hat{\mathbf{y}}\right] + \zeta\hat{\mathbf{z}}$$

$$\mathbf{v}(r,\theta,\zeta) = u(r,\theta)\hat{\mathbf{r}} + v(r,\theta)\hat{\boldsymbol{\theta}} + w(r,\theta)\hat{\mathbf{z}}$$

$$\nabla = \hat{\mathbf{r}}\frac{\partial}{\partial r} + \hat{\boldsymbol{\theta}}\frac{1}{r}\frac{\partial}{\partial \theta} + \hat{\mathbf{z}}\left(\frac{\partial}{\partial \zeta} - \nu\frac{\partial}{\partial \theta}\right)$$

$$\cdots$$

$f(\theta)=\cos(2\theta)$



Double series expansion in $(\varepsilon\nu, \nu^{-1})$ gives

$$\frac{U}{\omega/\nu} = \frac{\varepsilon^2}{2}J_N + \varepsilon^4\left(-\frac{1}{2}\nu^3N^4 + \nu^2\frac{3}{8}N^3\right) + O\left(\varepsilon^4\nu + \varepsilon^6\nu^6\right)$$

$$f(\theta) = \cos(N\theta)$$

Li & Spagnolie, *Phys. Fluids*, 2014 & 2015

What tools do we have? Lots.

Linear PDEs
Green's functions
Moment expansion / method of reflections / method of images
Boundary integral representation
Slender body theory
Fast algorithms
.
.
.

Main points I want to highlight:

Physical ideas:

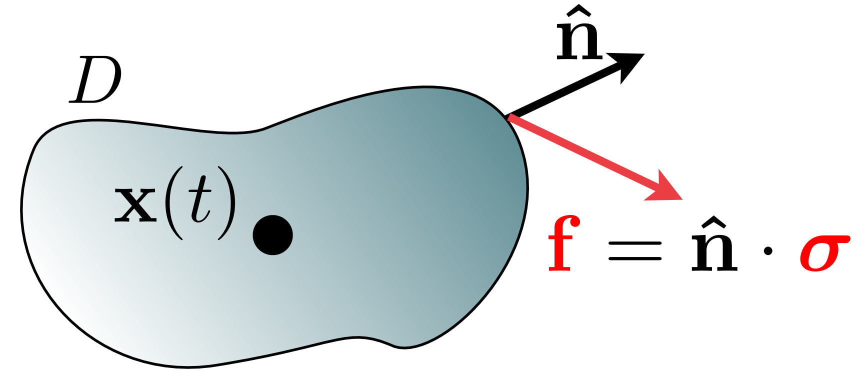
1. Kinematic reversibility / Scallop theorem
2. Quasi-static dynamics
3. Drag anisotropy of slender bodies
4. Stochastic (e.g. run-and-tumble) trajectories
5. Inside the flagellum: flagellin/polymorphism, microtubules/axoneme

Mathematical tools:

1. "Stokeslet" fundamental solution (Green's function) and its derivatives
2. A boundary-integral representation*
3. Multipole expansion in the far-field: bacteria as force-dipoles.
4. Slender-body theory for thin filaments (flagella, cilia, etc.)

Dynamics are quasi-static. Swimming is essentially force/torque-free at any moment.

$$m\ddot{\mathbf{x}} = \sum \mathbf{F}$$



$$\sum \mathbf{F} = \mathbf{F}_{ext} + \int_D \mathbf{f}\, dS$$

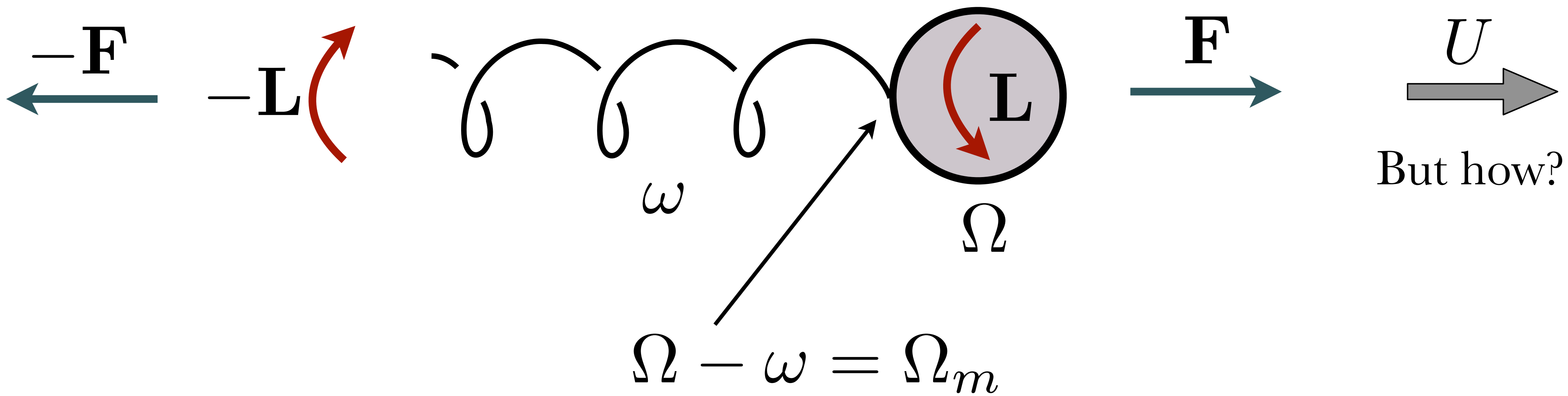
Scaling lengths, velocities on L, U as before, and scaling forces on $\mu L U$, we find

$$\cancelto{\mathbf{0}}{\mathrm{Re}\left(\frac{m}{\rho \mathrm{Vol}}\right)\left(\frac{\mathrm{Vol}}{L^3}\right)\ddot{\mathbf{x}}^*} = \frac{1}{\mu U L}\mathbf{F}_{ext} + \int_{D^*} \mathbf{f}^*\, dS^*$$

The body is in equilibrium at every moment. Even if $\mathbf{F}$, $\mathbf{f}$ are changing in time.
(Changes are slower than the viscous dissipation timescale.)

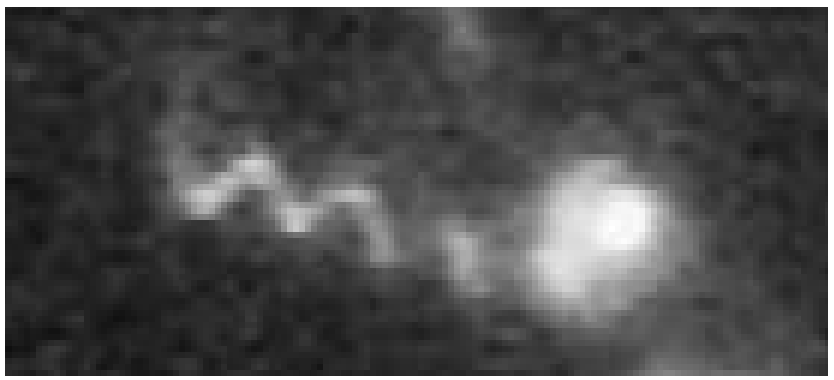
And if $|\mathbf{F}_{\mathbf{ext}}|/(\mu U L) \ll 1$, then $\int_{D^*} \mathbf{f}^*\, dS^* = \mathbf{0}$. Example: E. coli has $|\mathbf{F}_g|/(\mu U L) \approx 10^{-2}$

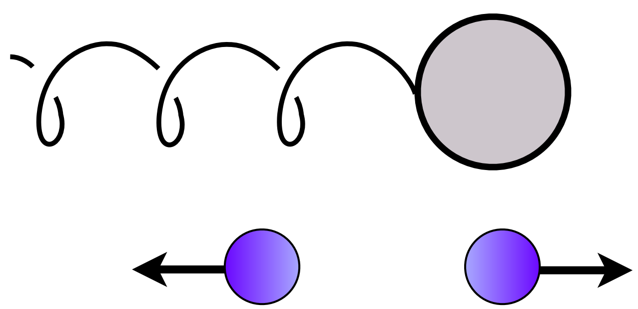
The torque-free constraint demands a counter-rotation



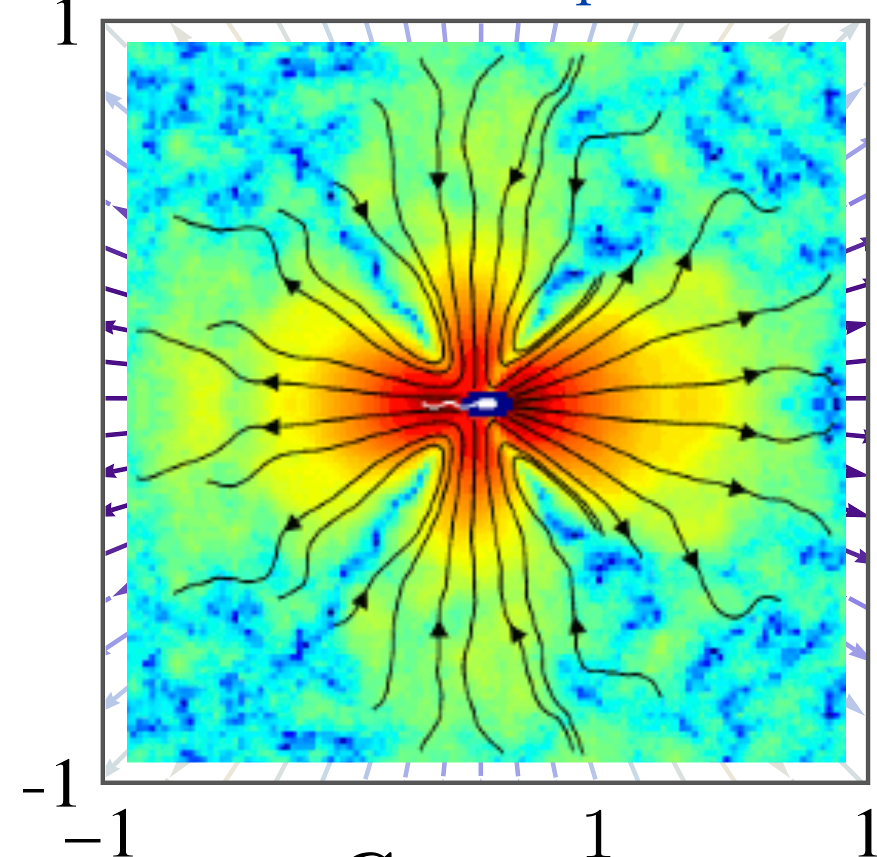
One answer: Don't worry about it!
Taking the long view:
mathematical modeling of swimming microbes via far-field hydrodynamics

E. coli, Turner, Ryu & Berg (J. Bacteriol. 2000)





Stokeslet dipole



$$\mathbf{G}_D \sim \frac{1}{R^2}$$

E. coli
Drescher et al. (PNAS 2011)

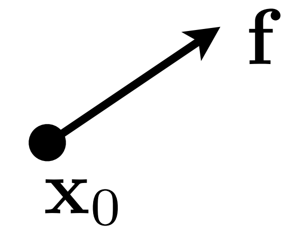
The leading order approximation of the fluid flow far from a neutrally buoyant body

To be more precise let's develop some mathematical tools, starting with the most important one.

The “Stokeslet” fundamental solution (Green’s function) is the key to everything.

What to do to a linear PDE?
Poke it.

$$-\nabla p + \mu \nabla \cdot \mathbf{u} + \mathbf{f}\delta(\mathbf{x}_0) = \mathbf{0}$$
$$\nabla \cdot \mathbf{u} = 0$$



By linearity, we must have $\mathbf{u}(\mathbf{x}) = \frac{1}{8\pi\mu}\mathbf{G}(\mathbf{x}-\mathbf{x}_0)\cdot\mathbf{f}$ $\quad p(\mathbf{x}) = \frac{1}{8\pi}\mathbf{\Pi}(\mathbf{x}-\mathbf{x}_0)\cdot\mathbf{f}$

Solving (e.g. by Fourier transform and inversion),

$$\mathbf{G}(\mathbf{x}) = \frac{1}{|\mathbf{x}|}\left(\mathbf{I} + \frac{\mathbf{x}\mathbf{x}}{|\mathbf{x}|^2}\right)$$

“Stokeslet” singularity

$$\mathbf{\Pi}(\mathbf{x}) = \frac{2\mathbf{x}}{|\mathbf{x}|^3}$$

$$(\mathbf{x}\mathbf{x})_{ij} = \mathbf{x}_i\mathbf{x}_j$$

(Dyadic product)

$$\mathbf{x}\mathbf{x}^T, \mathbf{x} \otimes \mathbf{x}$$

Read Pozrikidis (1992)

Derivatives of the Stokeslet are also solutions to the Stokes equations.

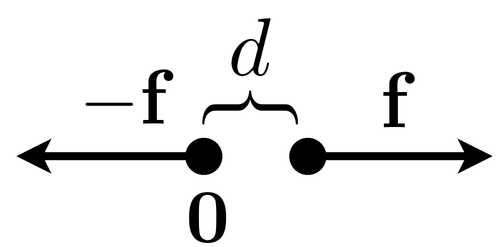
Linear PDE —> Linear combinations of Stokeslets also solve the primary equations

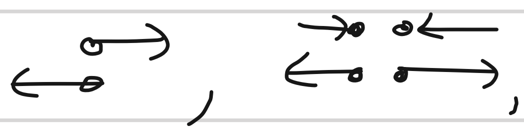
This includes derivatives (as differentiation is a linear operation)

$$\mathbf{u} = \frac{1}{d}\left(\mathbf{G}(\mathbf{x} - d\hat{\mathbf{x}}) \cdot \mathbf{f} - \mathbf{G}(\mathbf{x}) \cdot \mathbf{f}\right) \underset{d \to 0}{\rightarrow} \hat{\mathbf{x}} \cdot \nabla_{\mathbf{x}_0}(\mathbf{G} \cdot \mathbf{f})$$

is a solution, too.

"Stokeslet dipole" or "force dipole"

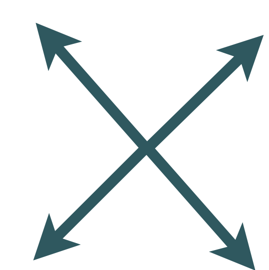


etc!  , ..., $\ldots\left(-\hat{y}\cdot\nabla(\underline{\underline{G}}\cdot\hat{x})\right.$, $\left.\hat{x}\cdot\hat{z}\cdot\hat{z}\cdot\nabla\nabla\nabla(\underline{\underline{G}}\cdot\hat{y})\ldots\right)$

How else can we poke the system?

$$-\nabla p_0 + \mu\nabla^2\mathbf{u}_0 = \mathbf{0}$$
$$\nabla \cdot \mathbf{u}_0 + M\delta(\mathbf{x}) = 0$$

$$\mathbf{u}_0 = \frac{-M\mathbf{x}}{4\pi|\mathbf{x}|^2}, \quad p_0 = 0$$



Source/sink

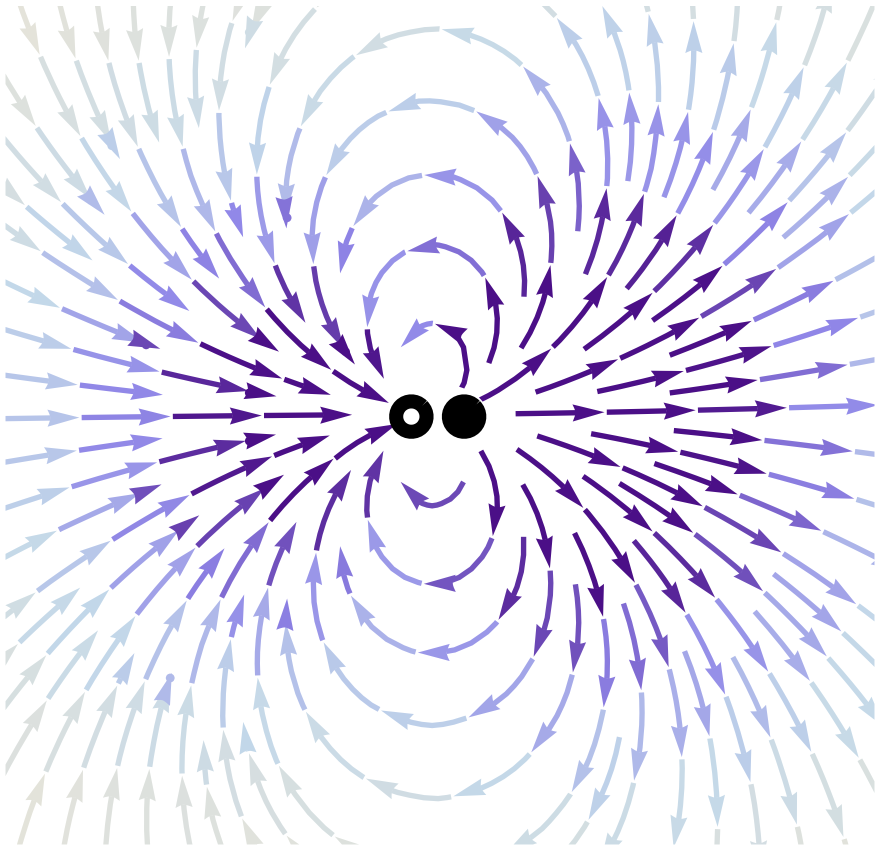
Including… all potential flow solutions

Since $\nabla^2 \mathbf{u}_0 = \mathbf{0}, \; p_0 = 0$

… all "potential flow" solutions (from infinite Reynolds number flow!) also solve the Stokes equations (zero Reynolds number flow!)

$$\mathbf{e} \cdot \nabla \mathbf{u}_0 = \frac{1}{|\mathbf{x}|^3} \left(-\mathbf{I} + \frac{3\mathbf{x}\mathbf{x}}{|\mathbf{x}|^2} \right) \cdot \mathbf{e} = \mathbf{D}(\mathbf{x}) \cdot \mathbf{e}$$

Source dipole/doublet

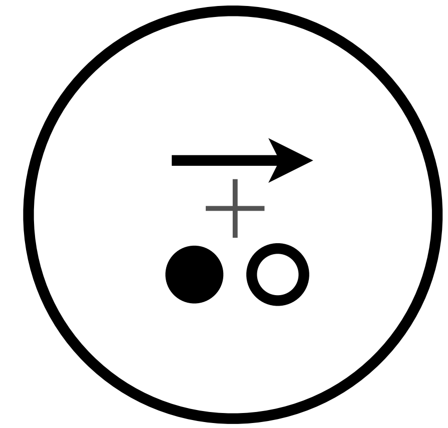


$\mathbf{e}$

The flow due to a moving sphere is simply represented by a combination of singular solutions

(!) A particularly interesting combination:

$$\mathbf{u} = \left(\mathbf{G} - \frac{a^2}{3}\mathbf{D}\right) \cdot \frac{\mathbf{F}}{8\pi\mu}$$



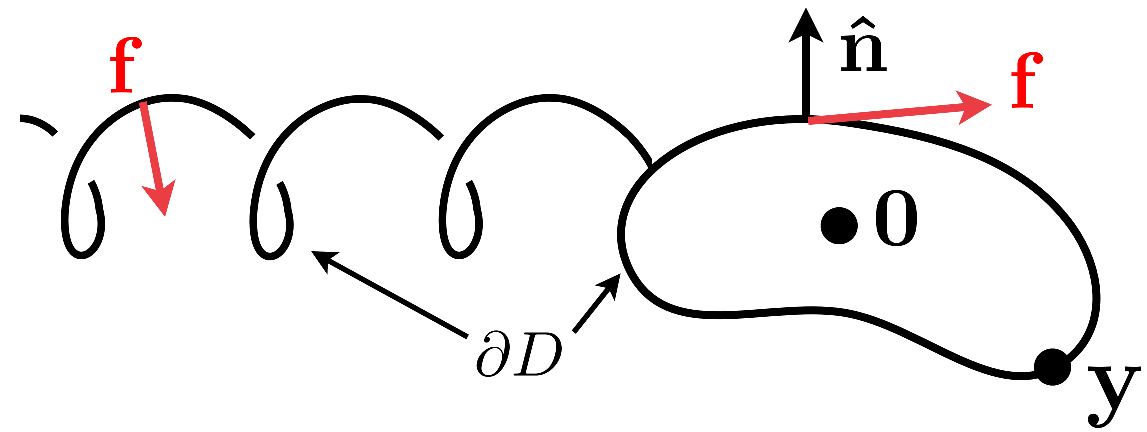
has $\mathbf{u}(r = a) = \dfrac{\mathbf{F}}{6\pi\mu a}$, ***constant!*** Call it $\mathbf{U}$. Then

$$\mathbf{F}_{fluid} = -6\pi\mu a\mathbf{U}$$

(Stokes Drag Law)

A more general multipole expansion often starts with a boundary integral representation

$$8\pi\mu\,\mathbf{u}(\mathbf{x}) = -\int_{\partial D} \mathbf{G}(\mathbf{x}-\mathbf{y})\cdot\mathbf{f}(\mathbf{y})\,dS_y$$



$$\mathbf{G}_{ij}(\mathbf{x},\mathbf{y}) = \frac{1}{|\mathbf{x}-\mathbf{y}|} + \frac{(x-y)_i(x-y)j}{|\mathbf{x}-\mathbf{y}|^3}$$

(Not the most general form… stay tuned for Shravan's lecture!)

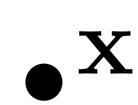
Now consider the flow at a point $\mathbf{x}$ far from the body.

Expanding around $\mathbf{0}$,

$$\mathbf{G}(\mathbf{x}-\mathbf{y}) = \mathbf{G}(\mathbf{x}-\mathbf{0}) + \mathbf{y}\cdot\nabla_y\mathbf{G}(\mathbf{x}) + \frac{1}{2}\mathbf{yy}:\nabla\nabla\mathbf{G}(\mathbf{x}) + \ldots$$

So

$$8\pi\mu\,\mathbf{u}(\mathbf{x}) = -\int_{\partial D}\left[\mathbf{G}(\mathbf{x}-\mathbf{0}) + \mathbf{y}\cdot\nabla_y\mathbf{G}(\mathbf{x}) + \frac{1}{2}\mathbf{yy}:\nabla\nabla\mathbf{G}(\mathbf{x}) + \ldots\right]\cdot\mathbf{f}(\mathbf{y})dS_y$$



Multipole expansion

$$8\pi\mu\, u_i(\mathbf{x}) = G_{ij}(\mathbf{x})F_j + \partial_k G_{ij}(\mathbf{y})S_{kj} + \partial_m \partial_k G_{ij}(\mathbf{x})M_{mkj} + \dots$$

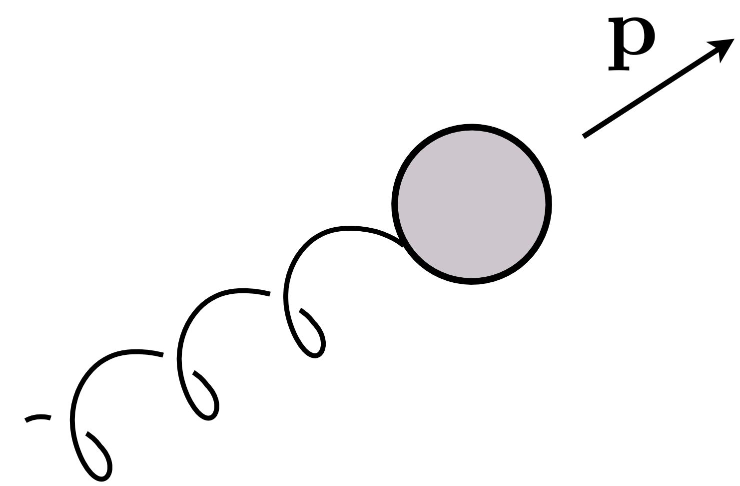
$$\mathbf{F} = -\int_{\partial D} \mathbf{f}(\mathbf{y})\, dS_y \qquad \mathbf{S} = -\int_{\partial D} \mathbf{y}\,\mathbf{f}(\mathbf{y})\, dS_y \qquad \mathbf{M} = -\frac{1}{2}\int_{\partial D} \mathbf{y}\mathbf{y}\,\mathbf{f}(\mathbf{y})\, dS_y$$

$$= \mathbf{F}_{\mathrm{ext}}$$

or

$$\mathbf{u}(\mathbf{x}) = \frac{1}{8\pi\mu}\mathbf{G}(\mathbf{x}) \cdot \mathbf{F} + \frac{1}{8\pi\mu}\nabla_y \mathbf{G}(\mathbf{x}) : \mathbf{S} + \dots$$

The pusher and puller business



Neutrally-buoyant? $\mathbf{F} = \mathbf{F}_{\text{ext}} = \mathbf{0}$

Axisymmetric? $\mathbf{S} = -\sigma \mathbf{p}\mathbf{p}$

$$\mathbf{u}(\mathbf{x}) = \frac{-\sigma}{8\pi\mu} \nabla_y \mathbf{G}(\mathbf{x}) : \mathbf{p}\mathbf{p} = \frac{-\sigma}{8\pi\mu} \mathbf{p} \cdot \nabla_y \left(\mathbf{G}(\mathbf{x}) \cdot \mathbf{p} \right)$$

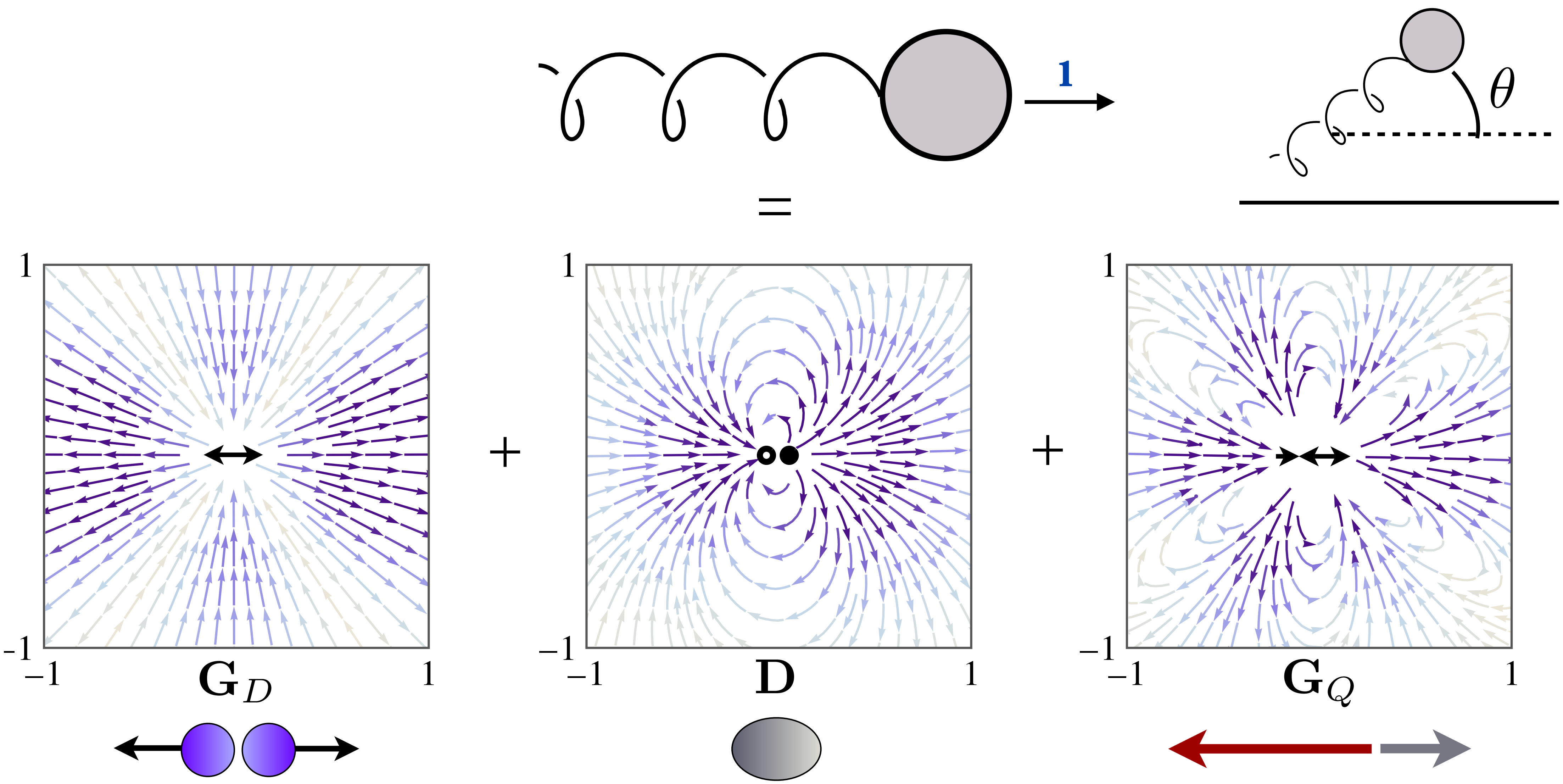
$\sigma < 0$: "Pusher"

$\sigma > 0$: "Puller"

(Stay tuned for Becca/David's lectures!)

More details enter as you approach the body

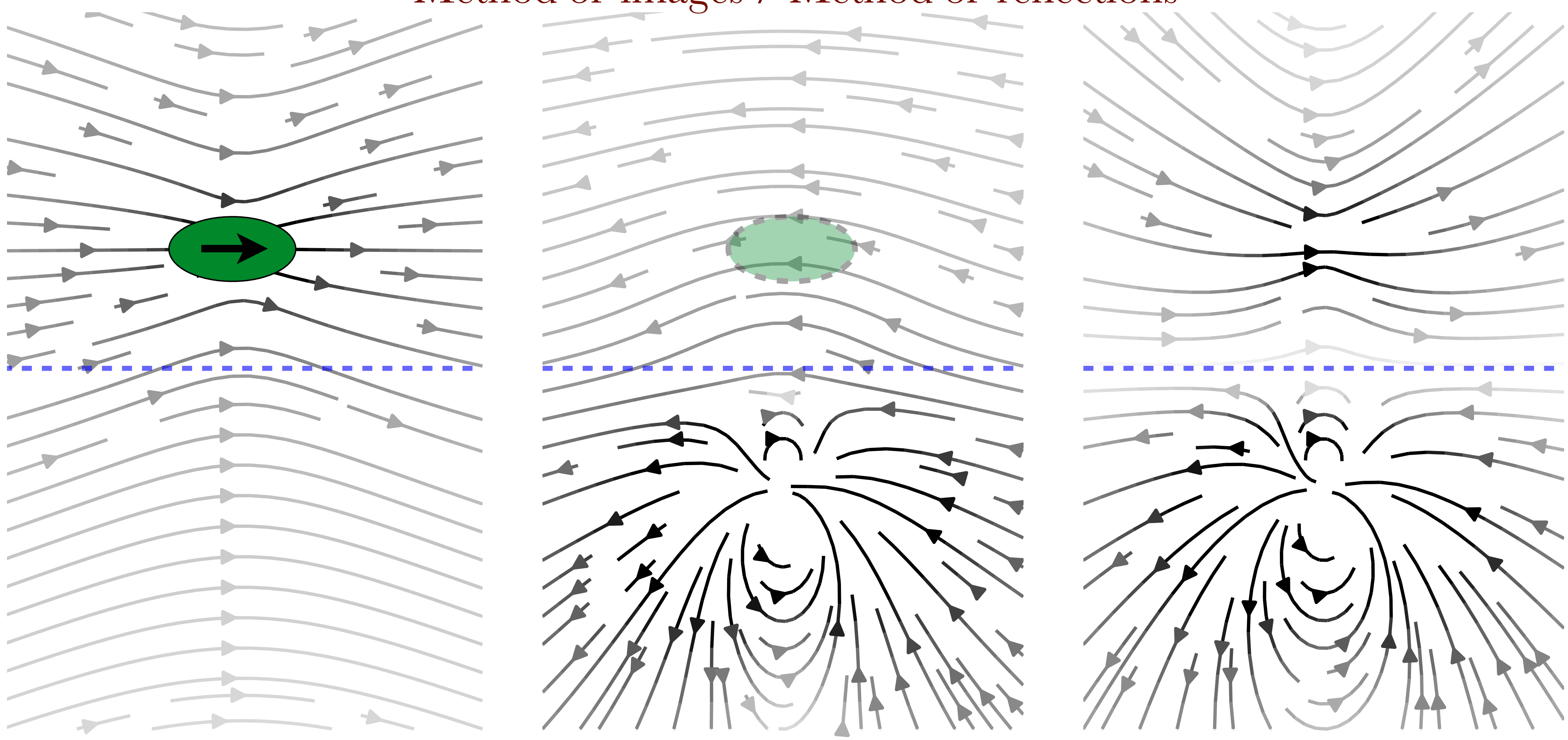
At a distance, a (phase-averaged) axisymmetric organism's far-field representation is:



$$\mathbf{u}(\mathbf{x}) = \underset{(R^{-2})}{\alpha \mathbf{G}_D} + \underbrace{\beta \mathbf{D} + \gamma \mathbf{G}_Q + \rho \mathbf{R}_D}_{(R^{-3})} + O(R^{-4})$$

This useful perspective provides insight into many phenomena. For example…
How does a wall affect the swimming trajectory? Use classical ideas from E&M…

Method of images / Method of reflections



$$G_{ij} f_j \quad + \quad G^*_{ij} f_j \quad = \quad \widetilde{G}_{ij} f_j$$

Stokeslet

Stokeslet image
(Blake 1971)

Zero velocity on the wall

See also: Faxén's Law, **Lorentz reflection theorem**

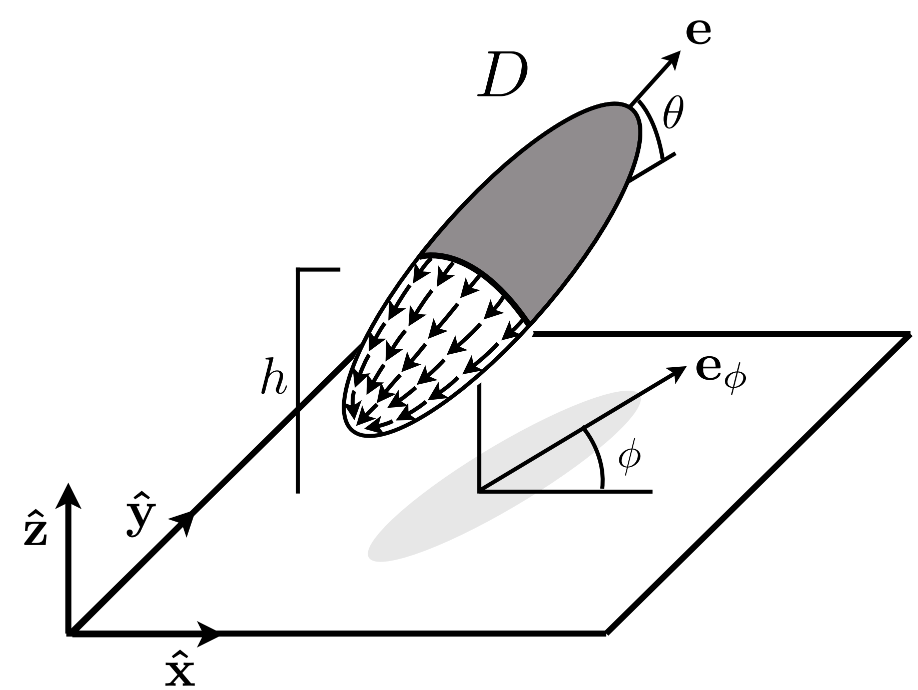
Computational interlude: boundary integral representation

$$8\pi\mu\,\mathbf{u}(\mathbf{x}) = \int_D \mathbf{G}(\mathbf{x},\mathbf{y})\cdot\mathbf{f}(\mathbf{y})\,dS_y + \mu\int_D \mathbf{u}(\mathbf{y})\cdot\mathbf{T}(\mathbf{x},\mathbf{y})\cdot\hat{\mathbf{n}}(\mathbf{y})\,dS_y$$

$$\mathbf{G}_{ij}(\mathbf{x},\mathbf{y}) = \frac{1}{|\mathbf{x}-\mathbf{y}|} + \frac{(x-y)_i(x-y)j}{|\mathbf{x}-\mathbf{y}|^3}$$

$$\mathbf{T}(\mathbf{x},\mathbf{y}) = -6\frac{(\mathbf{x}-\mathbf{y})(\mathbf{x}-\mathbf{y})(\mathbf{x}-\mathbf{y})}{R^5}$$

"Stresslet" singularity



Boundary integral representation with images

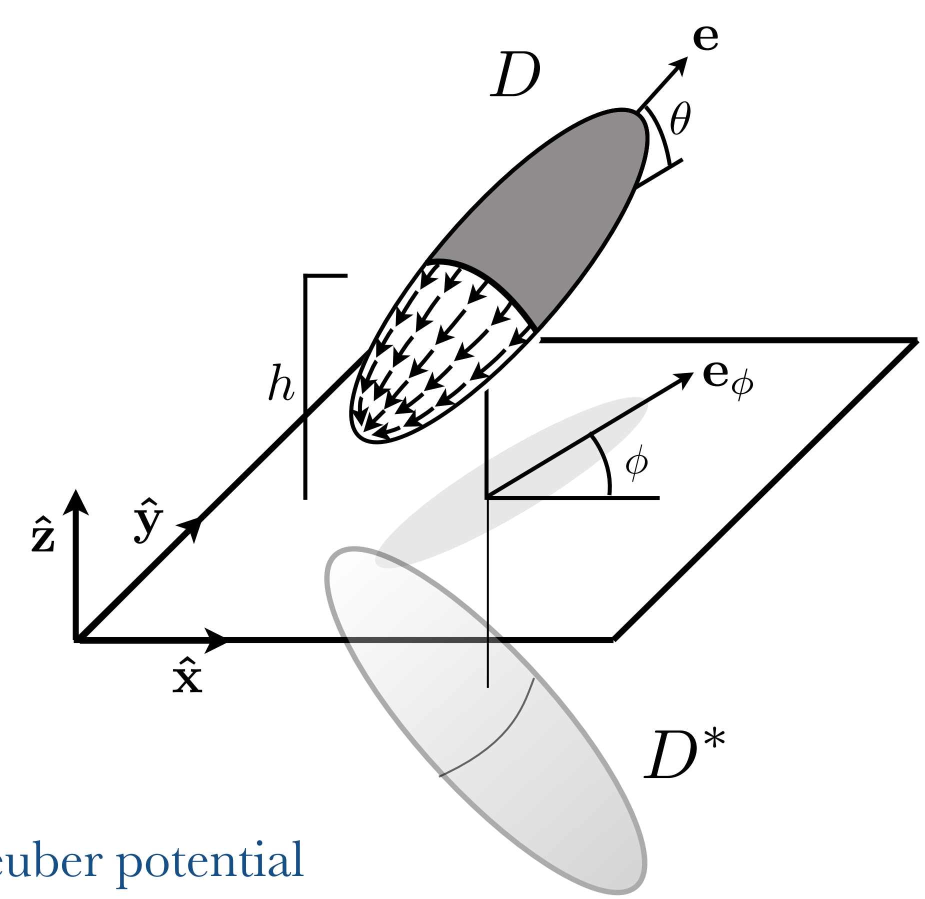
$$8\pi\mu\,\mathbf{u}(\mathbf{x}) = \int_D \mathbf{G}(\mathbf{x},\mathbf{y})\cdot\mathbf{f}(\mathbf{y})\,dS_y + \mu\int_D \mathbf{u}(\mathbf{y})\cdot\mathbf{T}(\mathbf{x},\mathbf{y})\cdot\hat{\mathbf{n}}(\mathbf{y})\,dS_y$$

$$+\int_{D^*} \mathbf{G}^*(\mathbf{x},\mathbf{y})\cdot\mathbf{f}(\mathbf{y})\,dS_y + \mu\int_{D^*} \mathbf{u}(\mathbf{y})\cdot\mathbf{T}^*(\mathbf{x},\mathbf{y})\cdot\hat{\mathbf{n}}\,dS_y$$

$$\mathbf{G}_{ij}(\mathbf{x},\mathbf{y}) = \frac{1}{|\mathbf{x}-\mathbf{y}|} + \frac{(x-y)_i(x-y)j}{|\mathbf{x}-\mathbf{y}|^3}$$

$$\mathbf{T}(\mathbf{x},\mathbf{y}) = -6\frac{(\mathbf{x}-\mathbf{y})(\mathbf{x}-\mathbf{y})(\mathbf{x}-\mathbf{y})}{R^5}$$

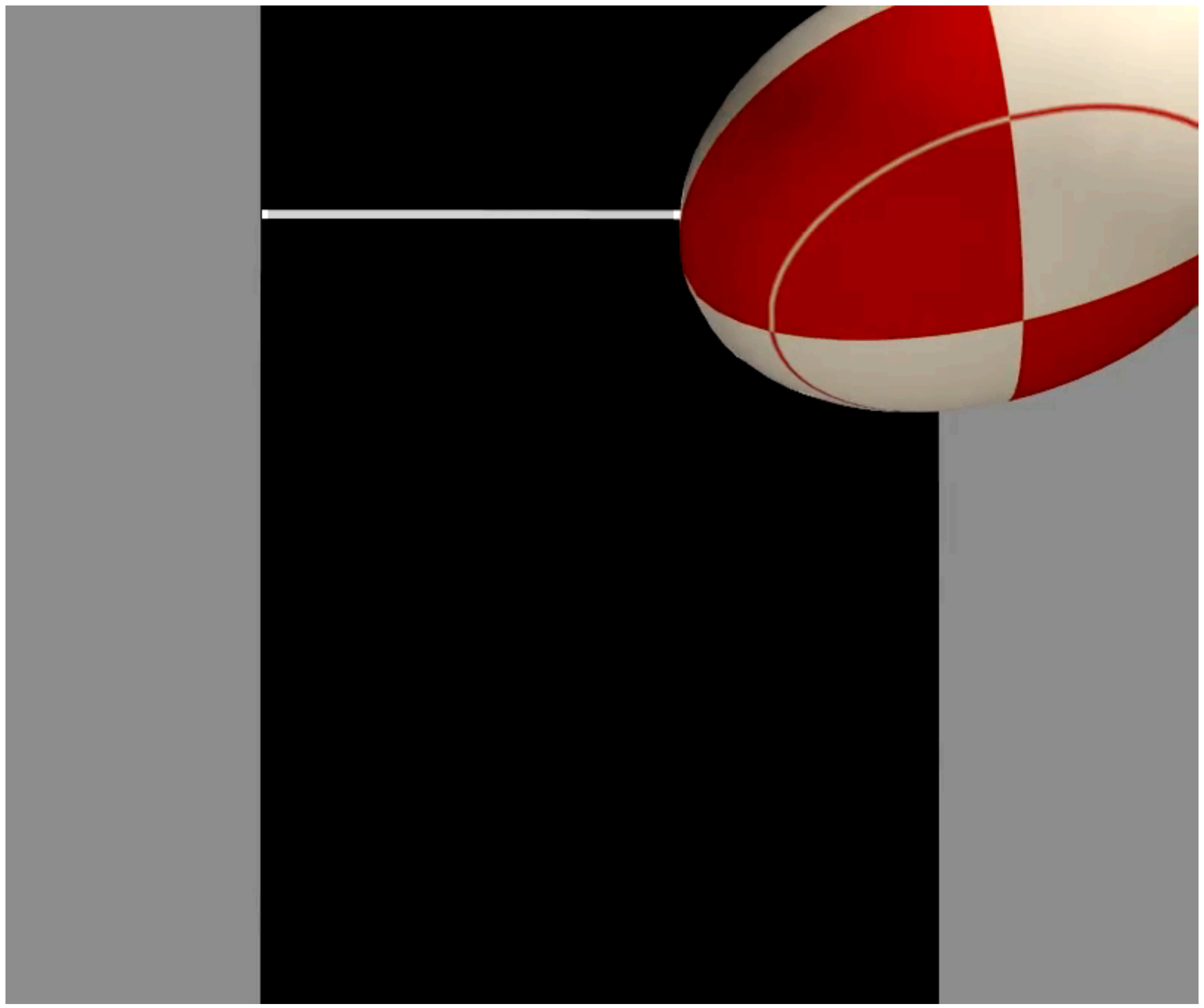
"Stresslet" singularity

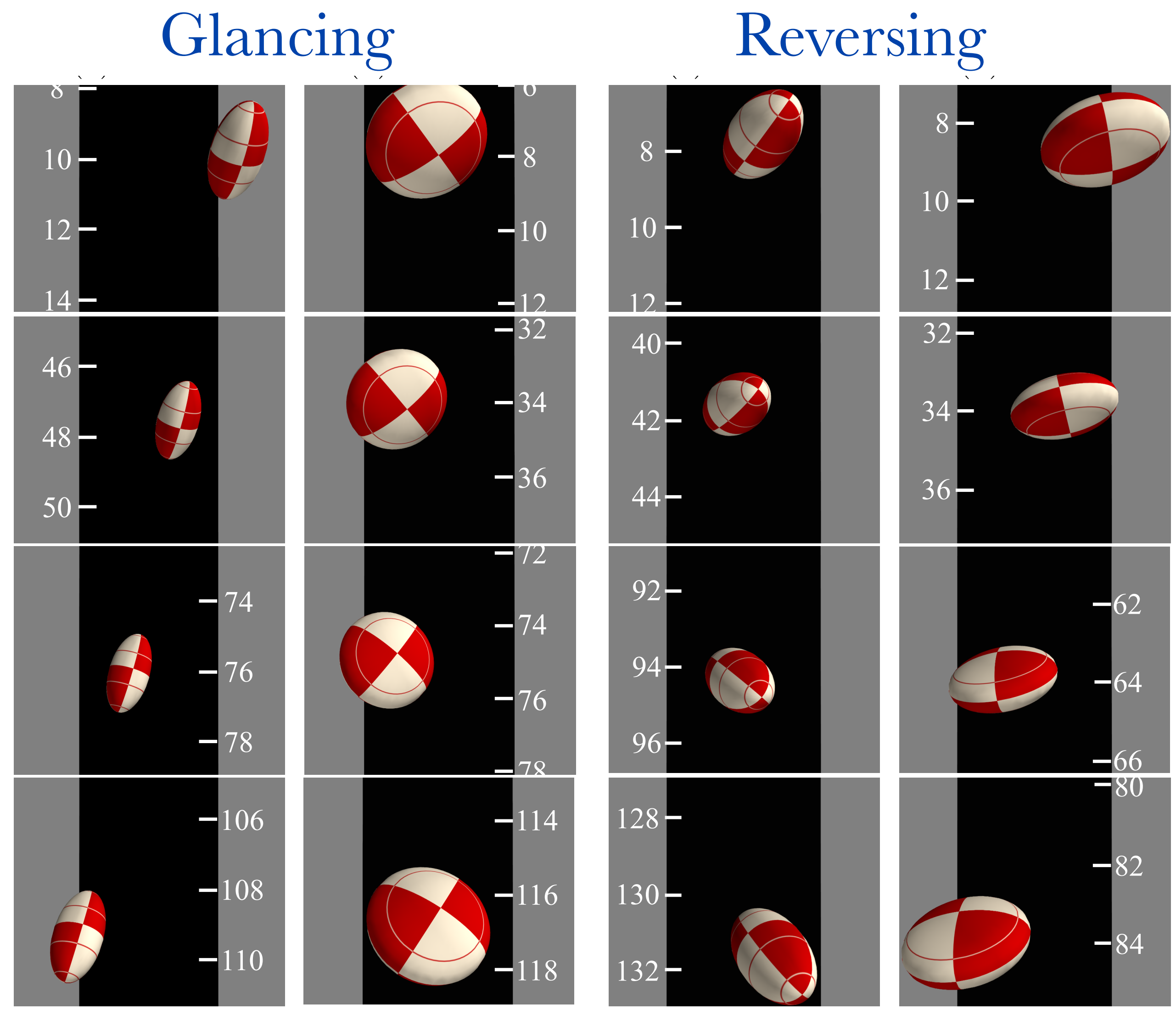


Spagnolie & Lauga (2012) - Brute force
Gimbutas, L. Greengard, S. Veerapaneni, (2015) - Papkovich-Neuber potential
Mitchell & Spagnolie, J. Comput. Phys. (2017) - Lorentz reflection theorem

$$\boldsymbol{T}^*_{ijk}(\boldsymbol{x},\boldsymbol{y}^*) = \frac{6\hat{X}_iX_jX_k}{|\boldsymbol{X}|^5} + 12x_3\frac{\beta_{ik}y_3X_j + \beta_{ij}y_3X_k - \delta_{jk}x_3\beta_{i\ell}X_\ell}{|\boldsymbol{X}|^5} - 60x_3y_3\beta_{i\ell}\frac{X_jX_kX_\ell}{|\boldsymbol{X}|^7},$$

Comparing to full numerical simulations,
analytical predictions are confirmed for all but the closest of wall-interactions





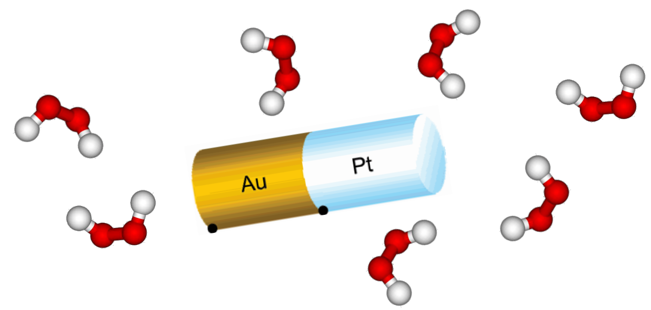
The far-field approximation is very accurate.

$$\mu/\mu_0 = 1 + \frac{5}{2}c + \cancel{7.6c^2} \rightarrow 6.95c^2$$ (Yoon & Kim, '87)

Batchelor & Green, J. Fluid Mech. (1972)

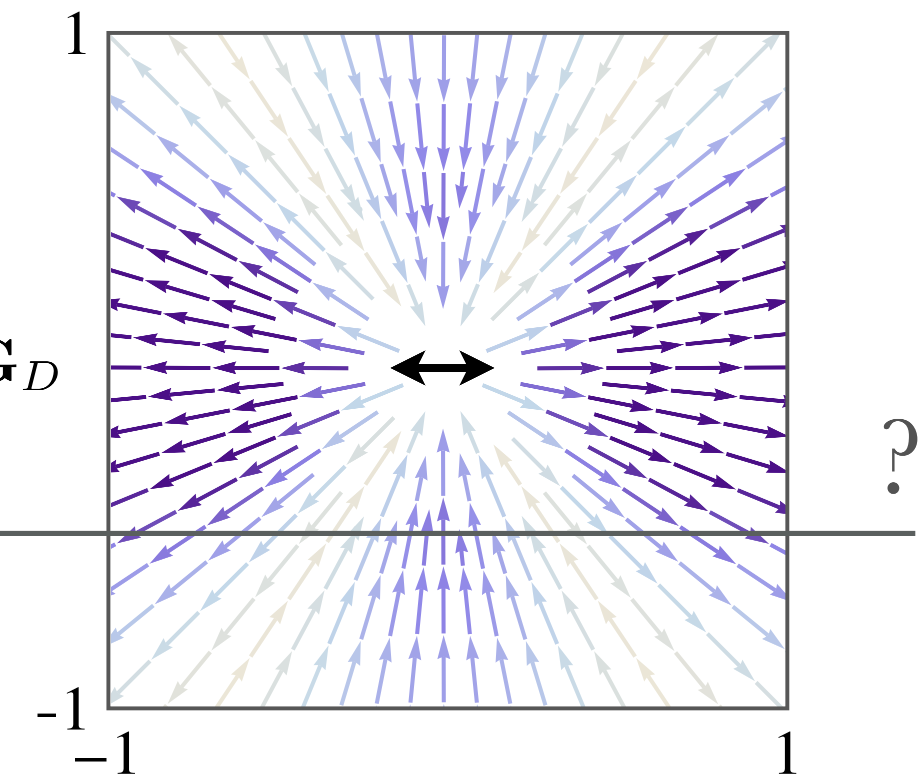
Mitchell & Spagnolie, J. Fluid Mech. 2015
Mitchell & Spagnolie, J. Comput. Phys. 2017

What is the effect of a nearby boundary on swimming trajectories?

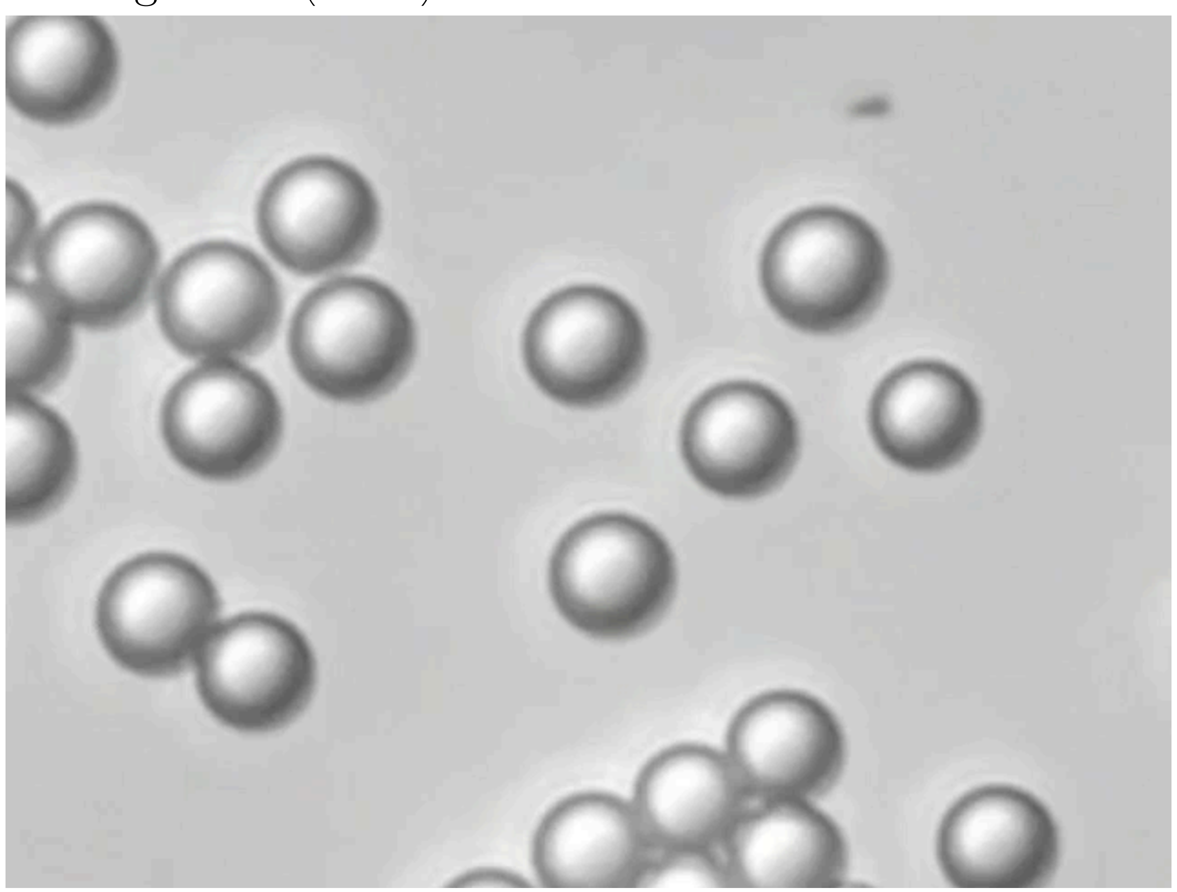


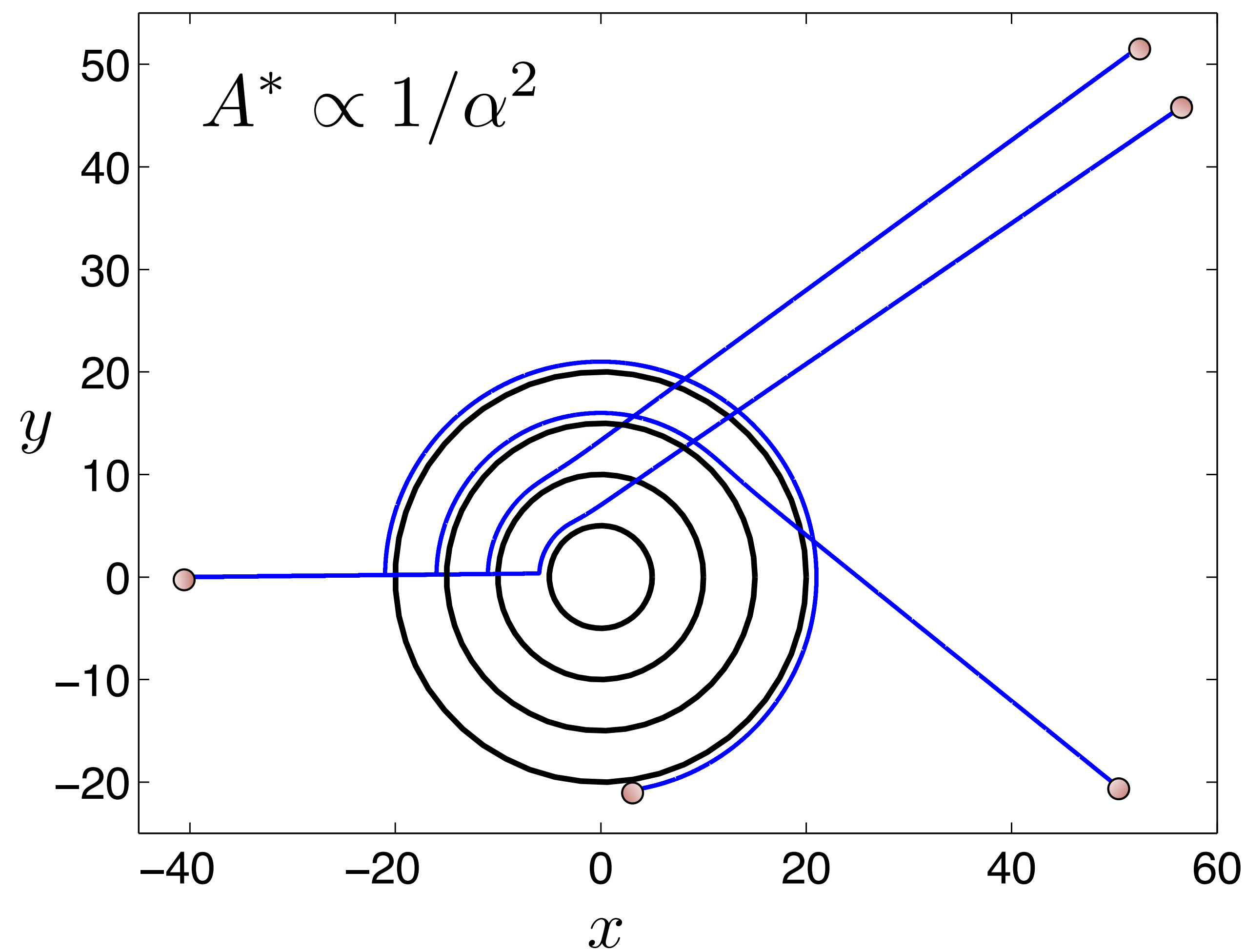
Paxton et al., (JACS, 2004).

$$\mathbf{u}(\mathbf{x}) = \alpha \mathbf{G}_D$$



Takagi et al. (2013)

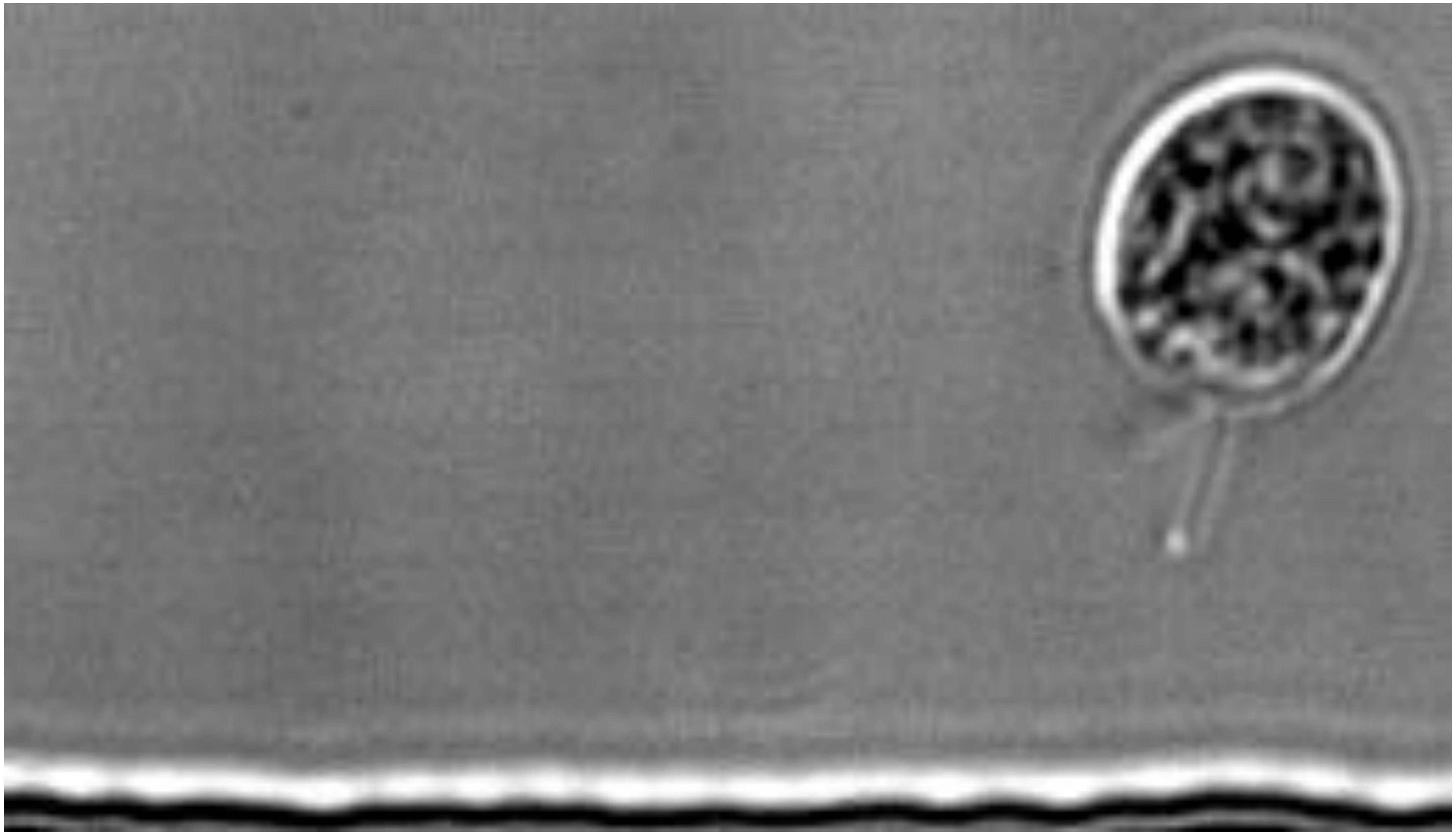




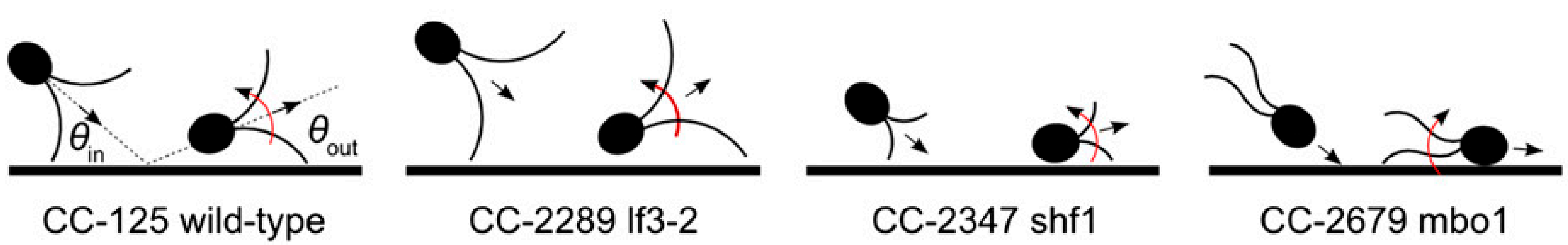
Takagi et al. (2013)
Spagnolie et al. (2015)

But don't lose sight of reality…

Chlamydomonas swimming near a surface



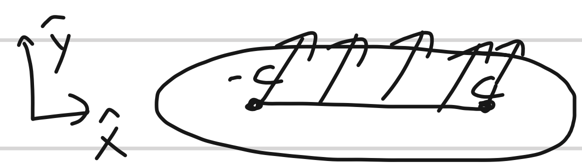
Kantsler et al. (PNAS 2012).



For more details you need… more tools!

☆ Singularity method

In "the singularity method" we try to find distributions of singularities internal to a body to satisfy no-slip, $\left(\vec{v}\big|_{\partial\Omega} = \vec{V} + \vec{\Omega} \times \vec{x}\right)$

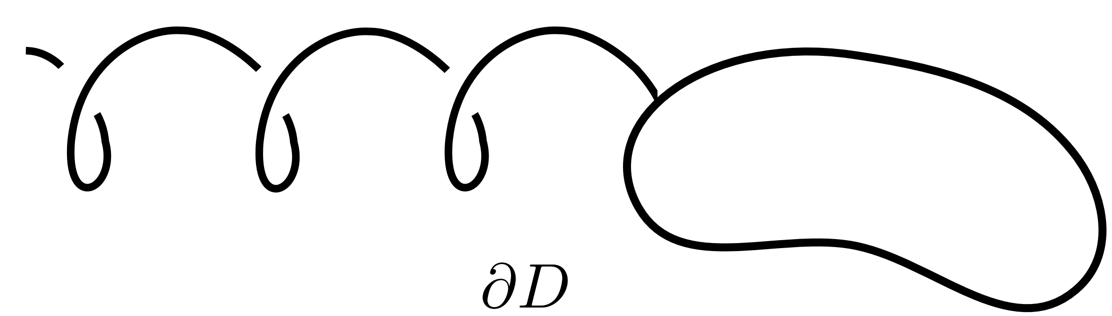
Prolate ellipsoid: 

Chwang + Wu "Part 2" (1975)

$$\vec{v} = \int_{-c}^{c} \alpha_1 \underline{\underline{G}} \cdot \hat{x} + \alpha_2 \underline{\underline{G}} \cdot \hat{y} \, ds + \int_{-c}^{c} (c^2 - s^2) \left[\beta_1 \underline{\underline{D}} \cdot \hat{x} + \beta_2 \underline{\underline{D}} \cdot \hat{y} \right] ds$$

Rotation, and linear background flows (shear/extensional) are done there too.

But that only gets us so far. How would we try to model this one?



Method 1: Compute.

Coming soon! Be patient!

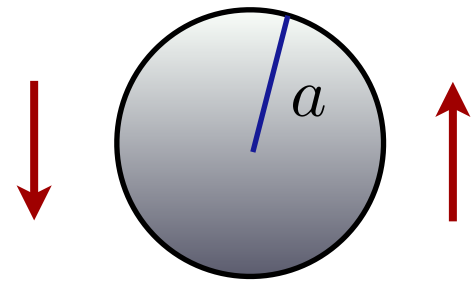
There are numerous numerical approaches
- Boundary integral methods
- Method of “Regularized Stokeslets”
- Various “immersed boundary methods”

Method 2: Exploit small parameters. For instance, the aspect ratio of the flagellum.

First let’s back up and talk about drag anisotropy.

The sedimentation speed of a sphere in a **viscous** fluid is linear in its surface area

$$F_g = \left(\frac{4}{3}\pi a^3\right)\Delta\rho g$$



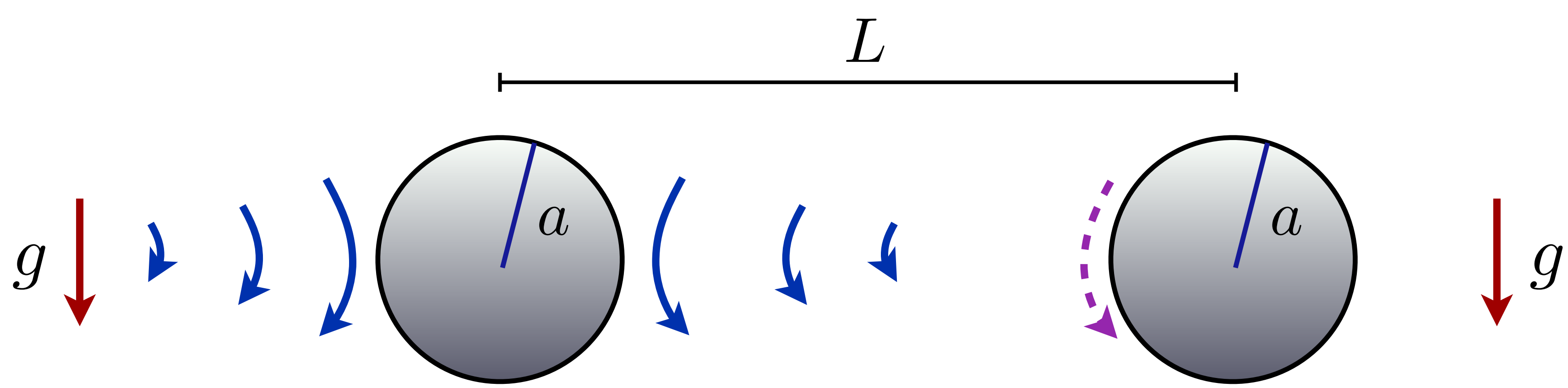
$$F_{Drag} = 6\pi\mu a U$$

"Stokes drag"

$$0 = F_g + F_{Drag}$$

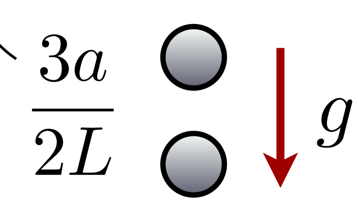
$$U = \frac{2a^2}{9\mu}\Delta\rho g$$

Hydrodynamic interactions increase the speed of multiple spheres in Stokes flow



$$U = \frac{2a^2}{9\mu}\Delta\rho g\left(1 + \frac{3a}{4L}\right) + O\left(\frac{a^2}{L^2}\right)$$

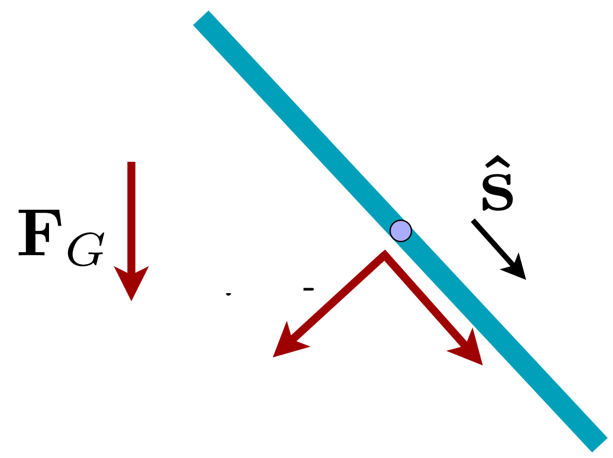
(far-field expansion)



(Torque balance also induces a rotation)

$$\Omega = \frac{a^3}{12\mu L^2}\Delta\rho g + O\left(\frac{a^3}{L^3}\right)$$

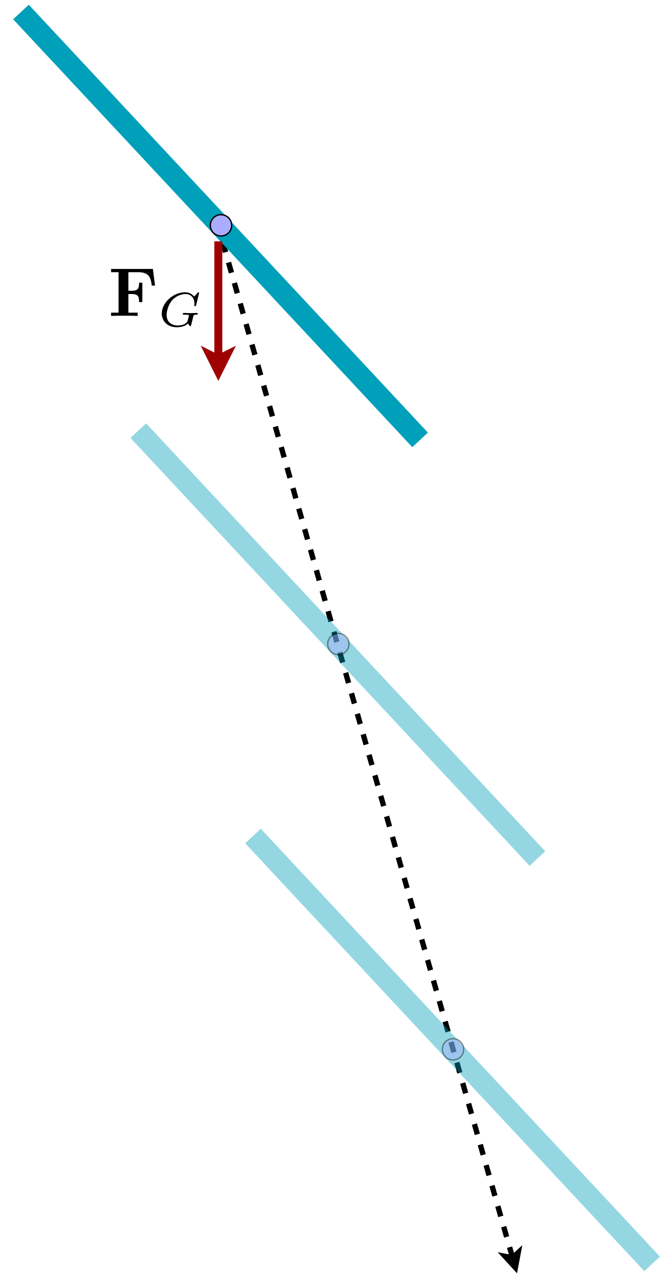
Hydrodynamic interactions lead to **drag anisotropy** of slender filaments



$$\mathbf{F}_g = \left[\xi_{||}\hat{\mathbf{s}}\hat{\mathbf{s}} + \xi_{\perp}(\mathbf{I} - \hat{\mathbf{s}}\hat{\mathbf{s}})\right] \cdot \mathbf{U} \qquad \frac{\xi_{\perp}}{\xi_{||}} \approx 2$$

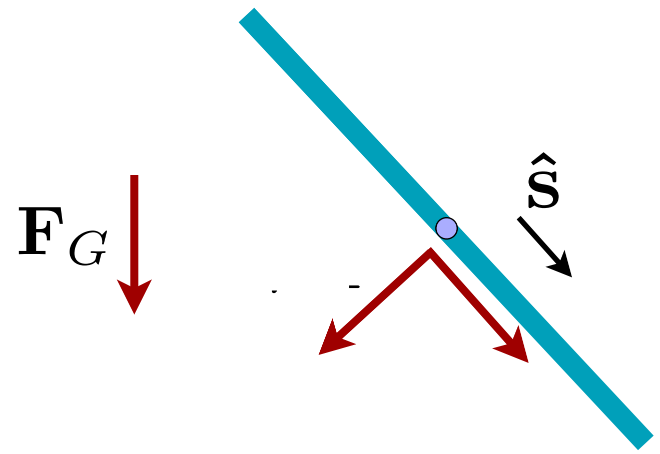
Filament aspect ratio $\varepsilon \lll 1$

Hydrodynamic interactions lead to **drag anisotropy** of slender filaments



$$\mathbf{F}_g = \left[\xi_{||}\hat{\mathbf{s}}\hat{\mathbf{s}} + \xi_{\perp}(\mathbf{I} - \hat{\mathbf{s}}\hat{\mathbf{s}})\right] \cdot \mathbf{U}$$

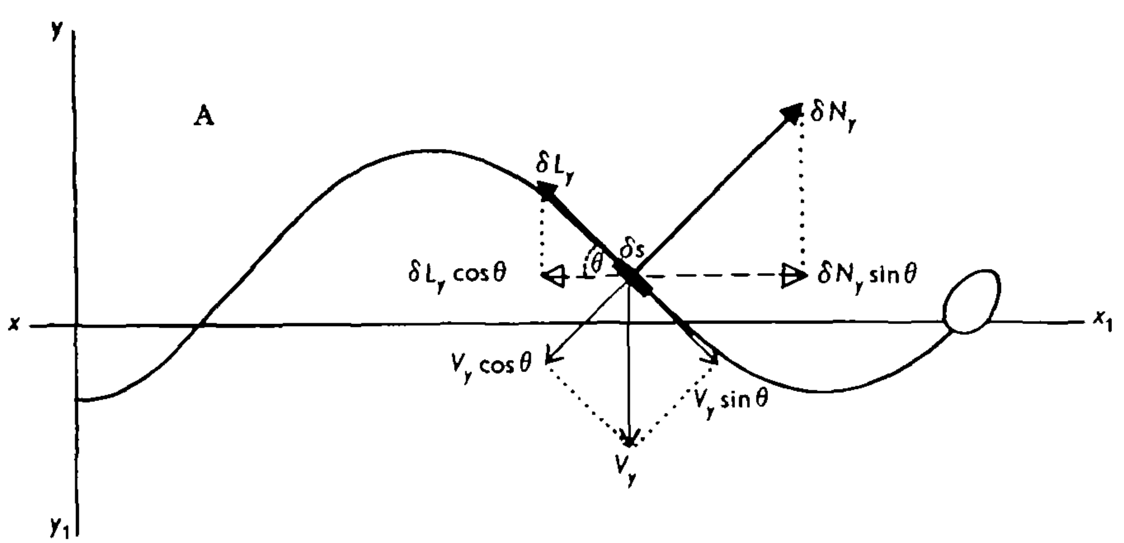
How to swim at zero Reynolds number: drag anisotropy



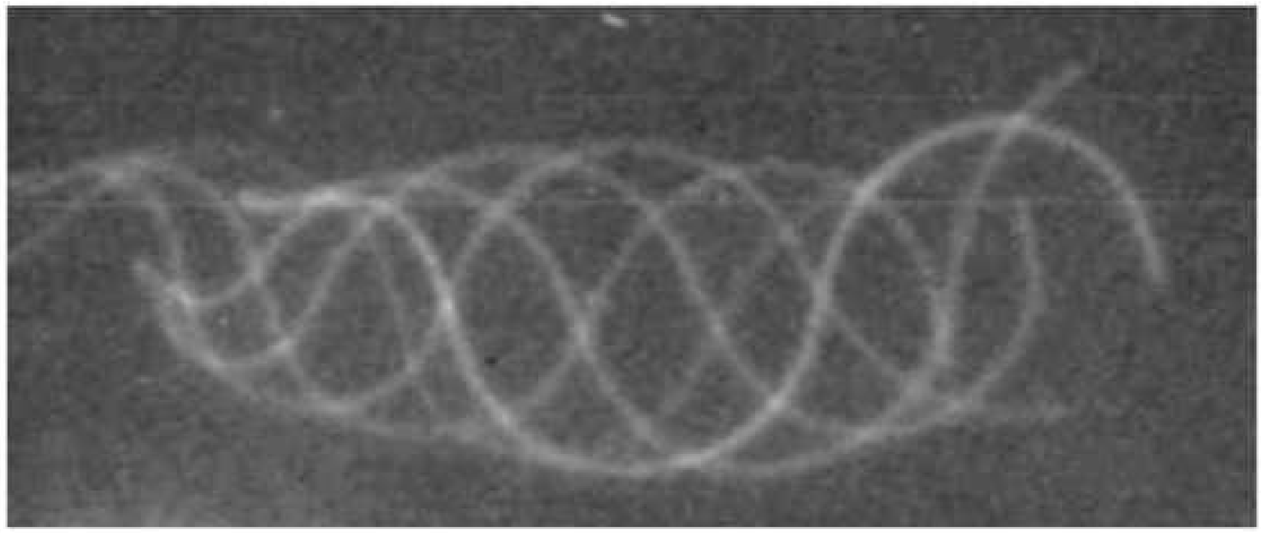
$$\mathbf{F}_g = \left[\xi_{||}\hat{\mathbf{s}}\hat{\mathbf{s}} + \xi_{\perp}(\mathbf{I} - \hat{\mathbf{s}}\hat{\mathbf{s}})\right] \cdot \mathbf{U} \qquad \frac{\xi_{\perp}}{\xi_{||}} \approx 2$$

Filament aspect ratio $\varepsilon \lll 1$

This is the basis of "Resistive Force Theory"

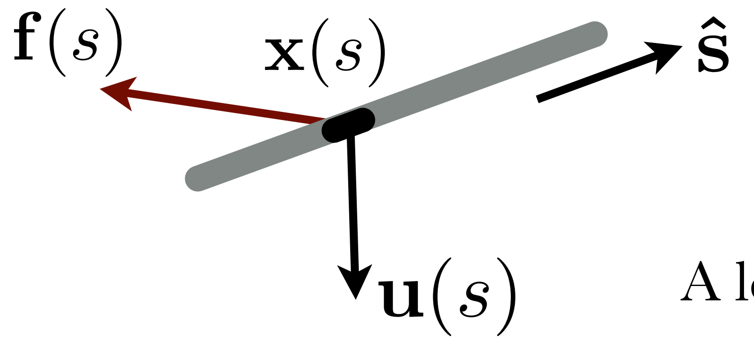


Gray & Hancock, (J. Exp. Biol. 1955)



Sea-urchin *Lytechinus* spermatozoon
C.J. Brokaw, Caltech

A first pass at slender filament hydrodynamics: resistive force theory



Hancock (1953), Gray & Hancock (1955)
to study sea-urchin spermatozoa

A local relation: $\mathbf{f}(s) = \left[\xi_{||}\hat{\mathbf{s}}\hat{\mathbf{s}} + \xi_{\perp}(\mathbf{I} - \hat{\mathbf{s}}\hat{\mathbf{s}})\right] \cdot \mathbf{u}(s)$

Example of usage:

$$\mathbf{x}(s) = (s, a\sin(ks - \omega t)) \qquad s \in (-\infty, \infty)$$

$$\mathbf{u}(s) = \mathbf{U} + \mathbf{x}_t = \mathbf{U} - a\omega\cos(ks - \omega t)\hat{\mathbf{y}}$$

If $\varepsilon = ak \ll 1, \quad \hat{\mathbf{s}} \approx (1, ak\cos(ks)) + O((ak)^2)$ (May as well set t=0)

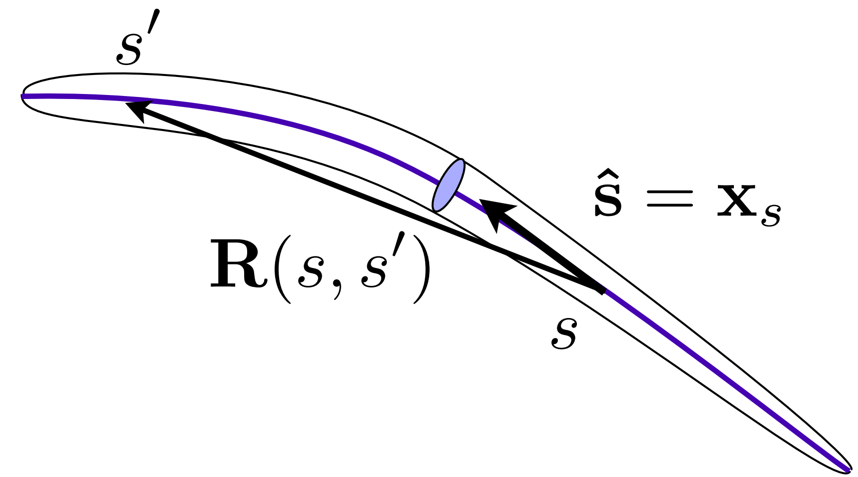
$$\mathbf{f}(s) = \left[\xi_{||}\begin{pmatrix} 1 & ak\cos(ks) \\ ak\cos(ks) & 0 \end{pmatrix} + \xi_{\perp}\begin{pmatrix} 0 & -ak\cos(ks) \\ -ak\cos(ks) & -1 \end{pmatrix}\right] \cdot (U, -a\omega\cos(ks))^{\mathsf{T}}$$

and now use $\displaystyle\int_0^{2\pi/k} \mathbf{f}(s)\, ds = \mathbf{0} \;\Rightarrow\; U = \frac{(ak)^2}{2}\left(\frac{\omega}{k}\right)\left(1 - \frac{\xi_{\perp}}{\xi_{||}}\right) < 0$ (Retrograde motion)

Pros: simple! Cons: Error is O(1). Great so long as $|\log\varepsilon| \gg 1$, or $\varepsilon \ll 10^{-10}$!

Stepping up the accuracy: slender-body theory
(matched asymptotics, relates to the singularity method)

$$\epsilon = \frac{a}{L} \ll 1 \longrightarrow$$



$$\mathbf{x}_t = -\mathbf{\Lambda}[\mathbf{f}] - \mathbf{K}[\mathbf{f}] + (\epsilon^2 \log(\epsilon))$$

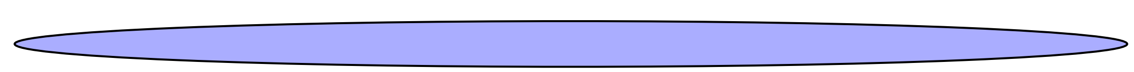
Local operator   Nonlocal integral operator

where $$\mathbf{\Lambda}[\mathbf{f}] = [(c(s)+1)\mathbf{I} + (c(s)-3)\hat{\mathbf{s}}(s)\hat{\mathbf{s}}(s)] \cdot \mathbf{f}(s)$$

$$\boldsymbol{K}[\boldsymbol{f}](s) = \int_0^1 \left(\frac{\boldsymbol{I} + \hat{\boldsymbol{R}}(s,s')\hat{\boldsymbol{R}}(s,s')}{|\boldsymbol{R}(s,s')|} \cdot \boldsymbol{f}(s') - \frac{\boldsymbol{I} + \hat{\boldsymbol{s}}(s)\hat{\boldsymbol{s}}(s)}{|s-s'|} \cdot \boldsymbol{f}(s) \right) \mathrm{d}s',$$

$$c(s) = \log\left(\frac{4s(1-s)}{\epsilon^2 r(s)^2}\right)$$

Special profile:



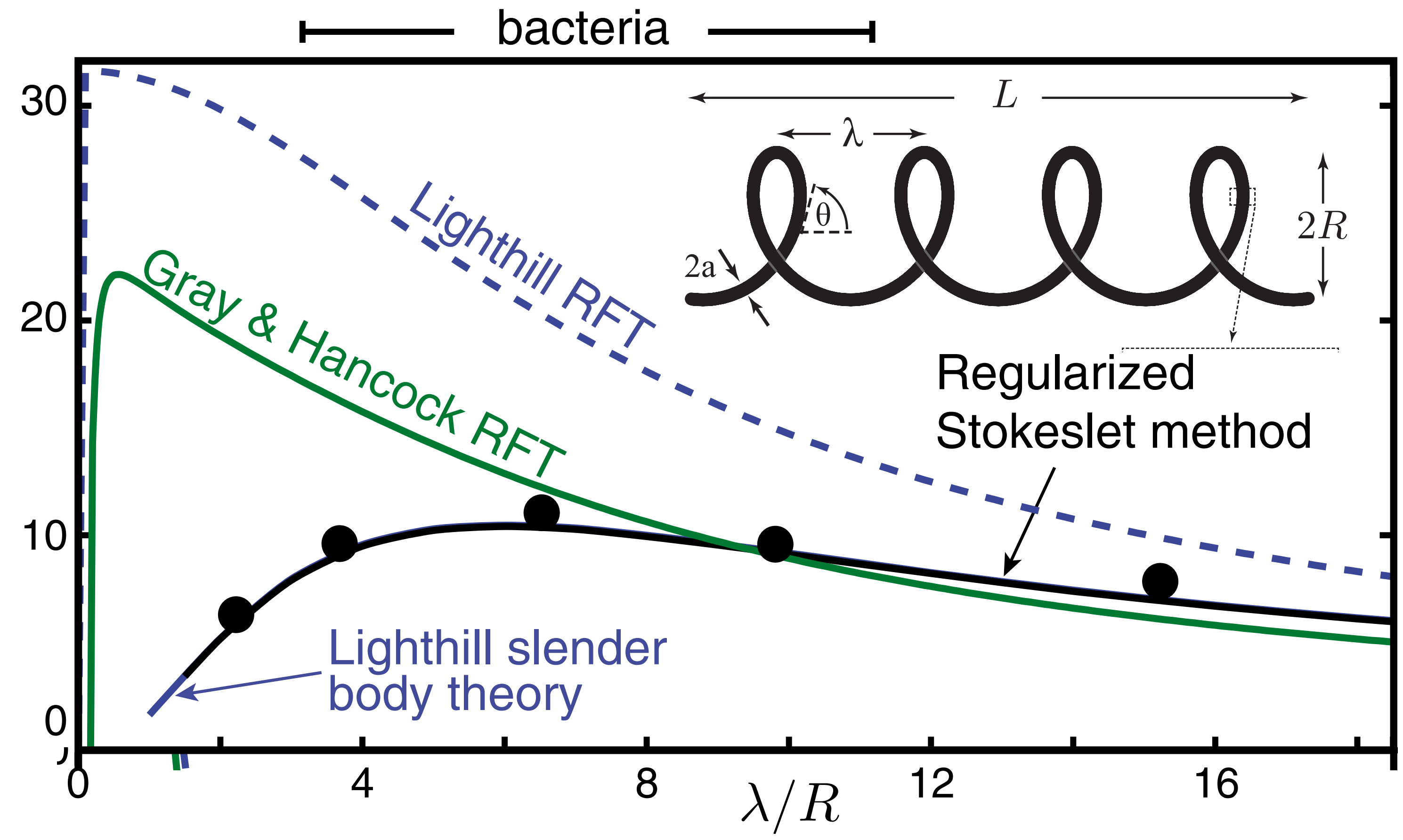
$$r(s) = \sqrt{4s(1-s)}$$

SBT is often the basis for high-accuracy
numerical simulations
and sometimes analysis (small amplitude)

$$\int_0^L \frac{\mathcal{L}_p(s') - \mathcal{L}_p(s)}{|s'-s|}\, ds' = \lambda_p \mathcal{L}_p(s)$$

(diagonalized by Legendre polynomials)

Health warning:



(helical pitch)

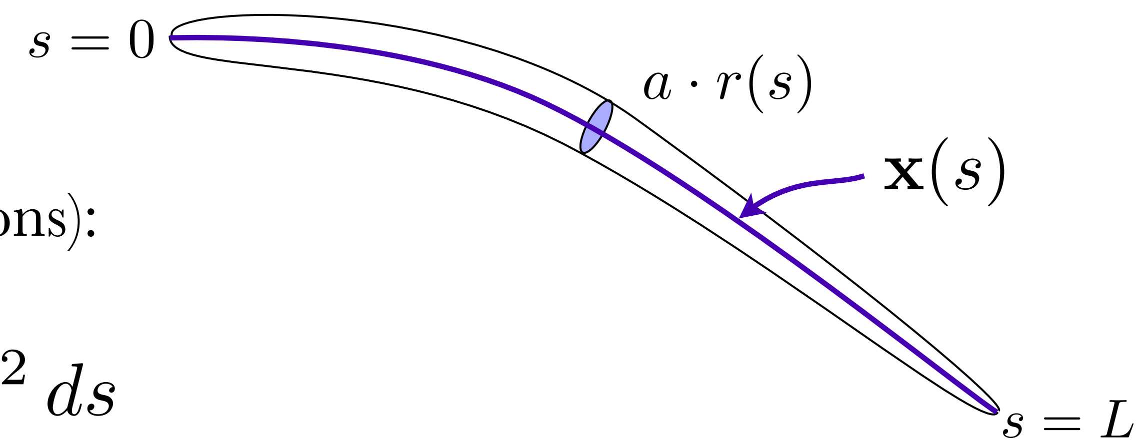
Johnson & Brokaw (1979)
Rodenborn et al., (2013)

What's **f** ?

Depends. Might be just like in the RFT calculation.
i.e. Rigid body dynamics assumed, use net-force on the body to infer **f**(s), but now via SBT.

But a richer class of problems links the local viscous traction to internal stresses in a continuously deformable filament.

Perhaps the force per unit length on the filament is found by the principal of virtual work. Quick example…



An inextensible Euler-Bernoulli beam (small deflections):

$$\mathcal{E} = \frac{B}{2}\int_0^L |\mathbf{x}_{ss}|^2\,ds + \int_0^L \frac{T(s)}{2}(|\mathbf{x}_s| - 1)^2\,ds$$

Dimensionless viscous drag:

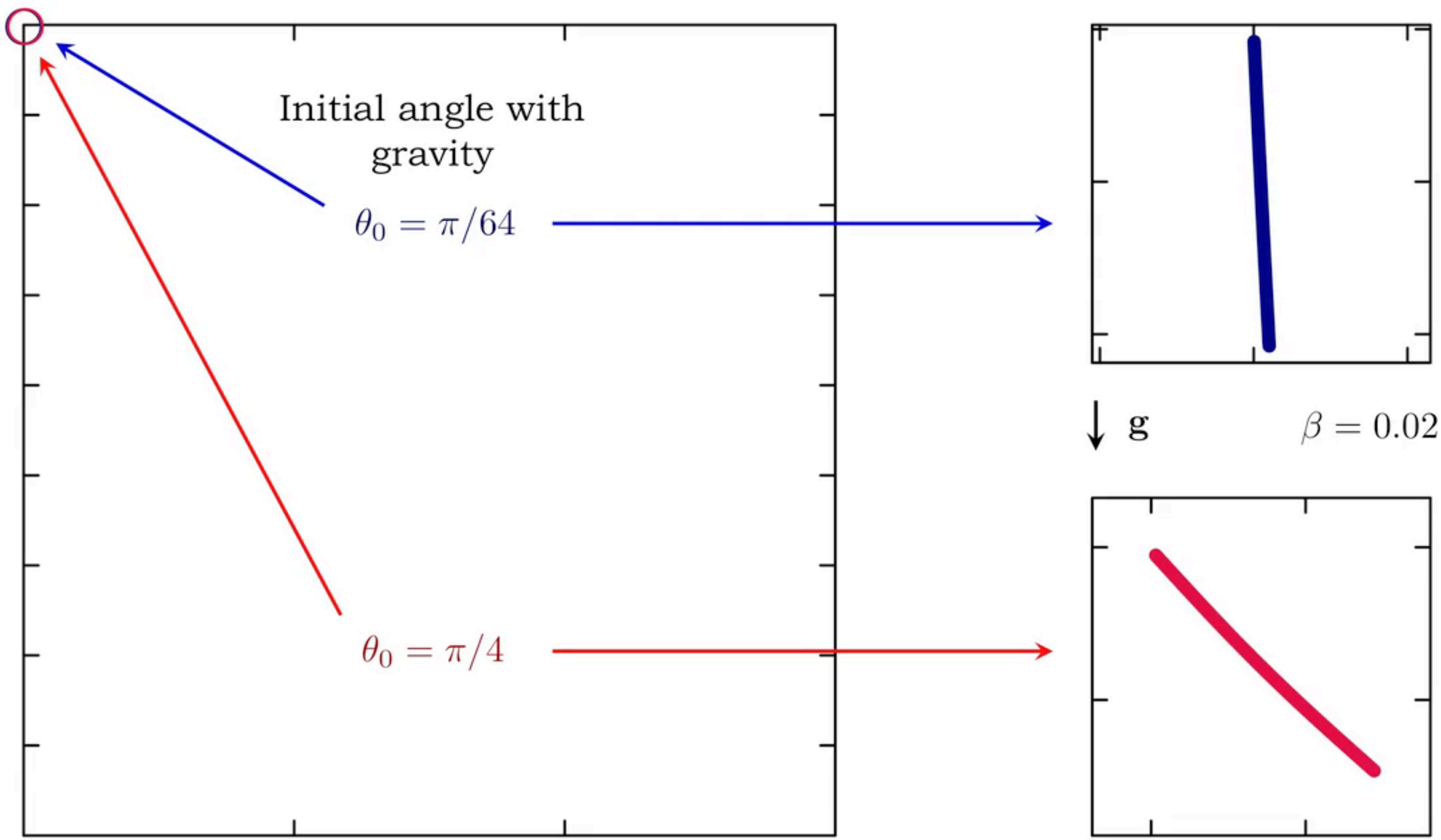
$$\mathbf{f}(s) = -\mathbf{F}_g(s) - (T(s)\mathbf{x}_s)_s + \beta(B(s)\mathbf{x}_{ss})_{ss}$$

Viscous drag | Gravity | Tension | Elasticity

$\beta \gg 1$: Stiff filaments (rods)

$\beta \ll 1$: Floppy filaments

Weakly flexible filaments sedimenting under gravity: shapes and trajectories slowly approach equilibrium



Xu & Nadim (1992)
Li et al. (2013)
Manikantan et al. (2014)

Eukaryotic vs. prokaryotic flagella: elastohydrodynamics

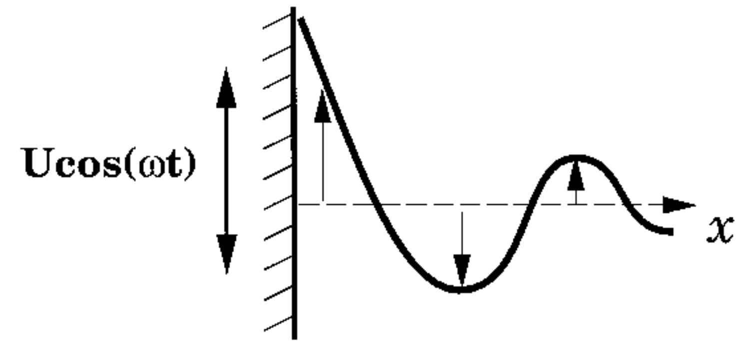
Bending vs. viscous forces

$$\mathcal{E}_{\text{bend}} = \frac{EI}{2}\int_0^L \kappa(s)^2\, ds$$

E Young's modulus

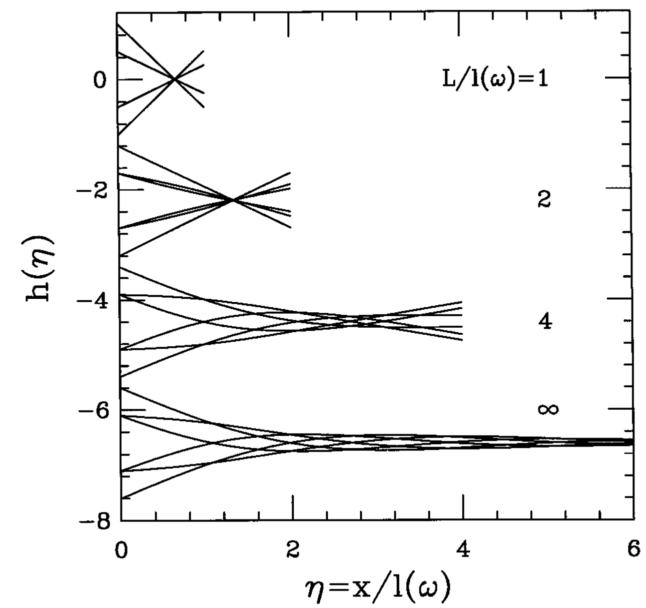
I Second inertial moment

κ Curvature

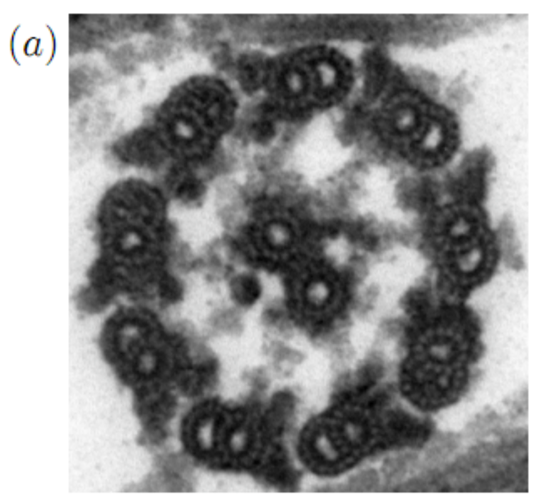


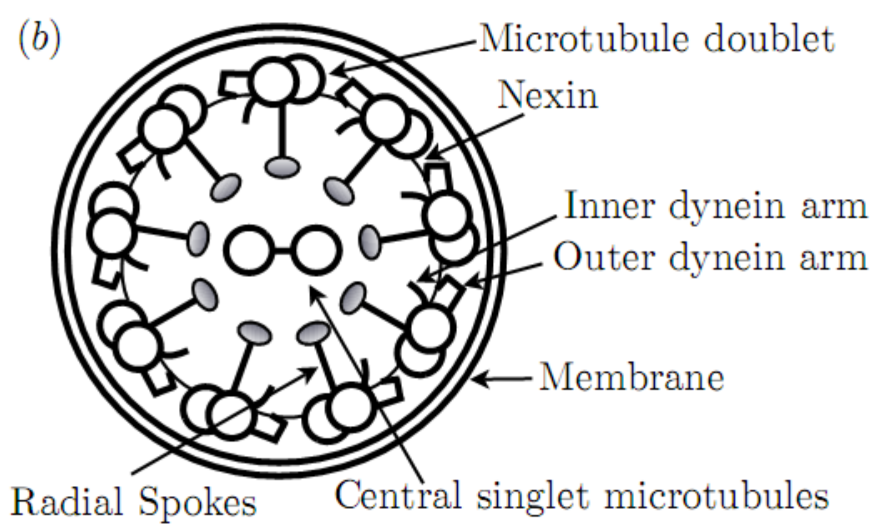
Wiggins et al. (Biophys J. 1998)

Exponentially decaying amplitude

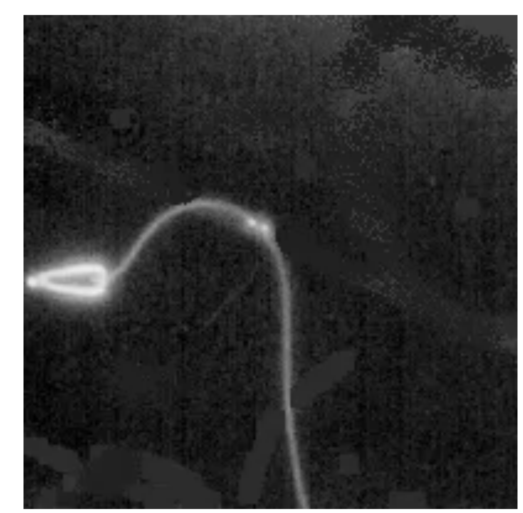


Planar waves (eukaryotic flagella) must be driven actively along the entire filament





9+2 axoneme
Brennen & Winet,
(Ann. Rev. Fluid Mech 1977)



Sea-urchin *Lytechinus* spermatozoon
C.J. Brokaw, Caltech

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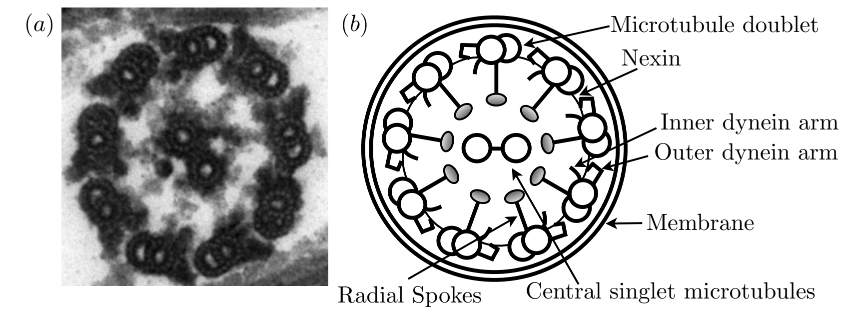

Generic aspects of axonemal beating

Sébastien Camalet and Frank Jülicher
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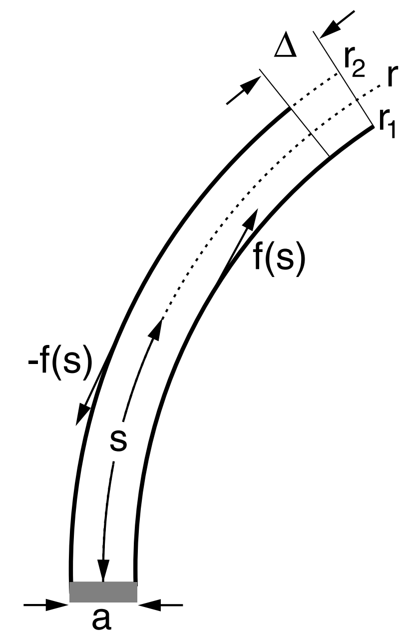


$$G \equiv \int_0^L \left[\frac{B}{2}C^2 + f\Delta + \frac{\Lambda}{2}\dot{\boldsymbol{r}}^2\right] \mathrm{d}s. \quad (C = \kappa)$$

$$\Delta = a\int_0^s \mathrm{d}s'\, C$$

$$\frac{\delta G}{\delta \boldsymbol{r}} = \partial_s[(B\dot{C} - af)\boldsymbol{n} - \tau\boldsymbol{t}]$$

$$\partial_t \boldsymbol{r} = -\left(\frac{1}{\xi_\perp}\boldsymbol{n}\boldsymbol{n} + \frac{1}{\xi_\parallel}\boldsymbol{t}\boldsymbol{t}\right)\cdot\frac{\delta G}{\delta \boldsymbol{r}}$$

Self-organized beating!

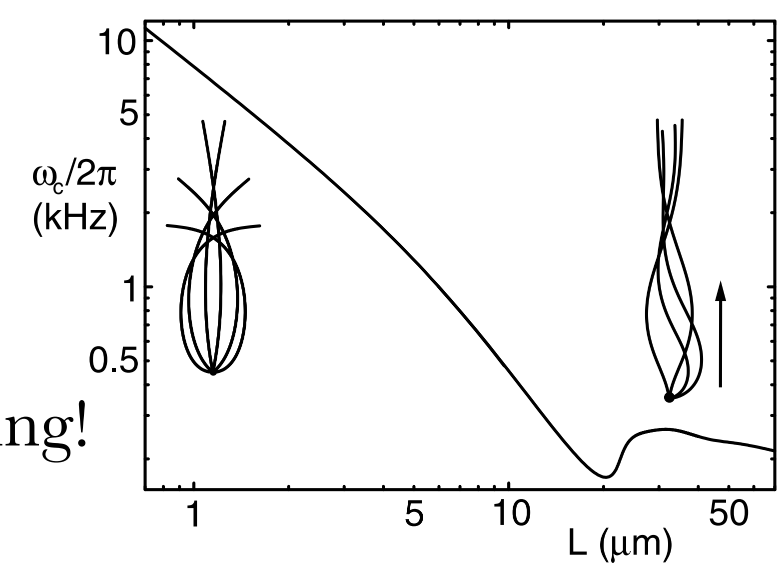
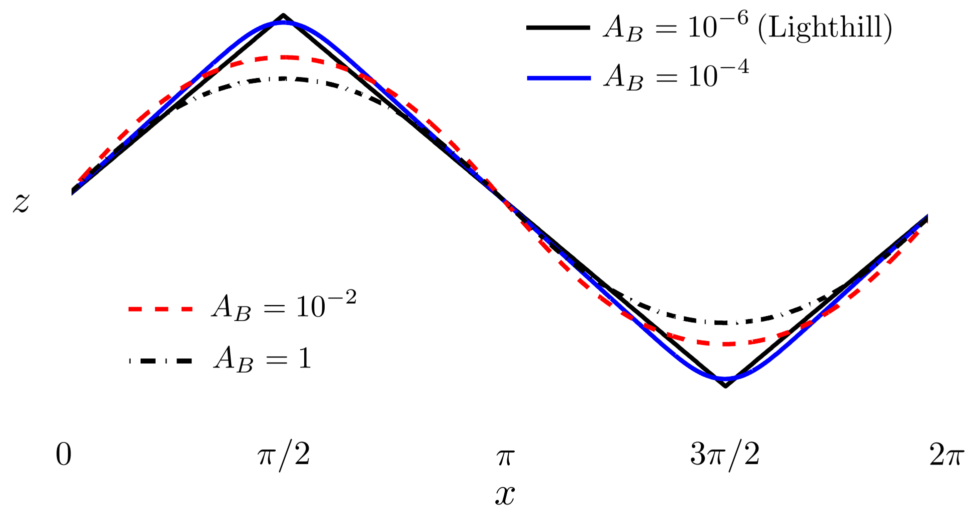


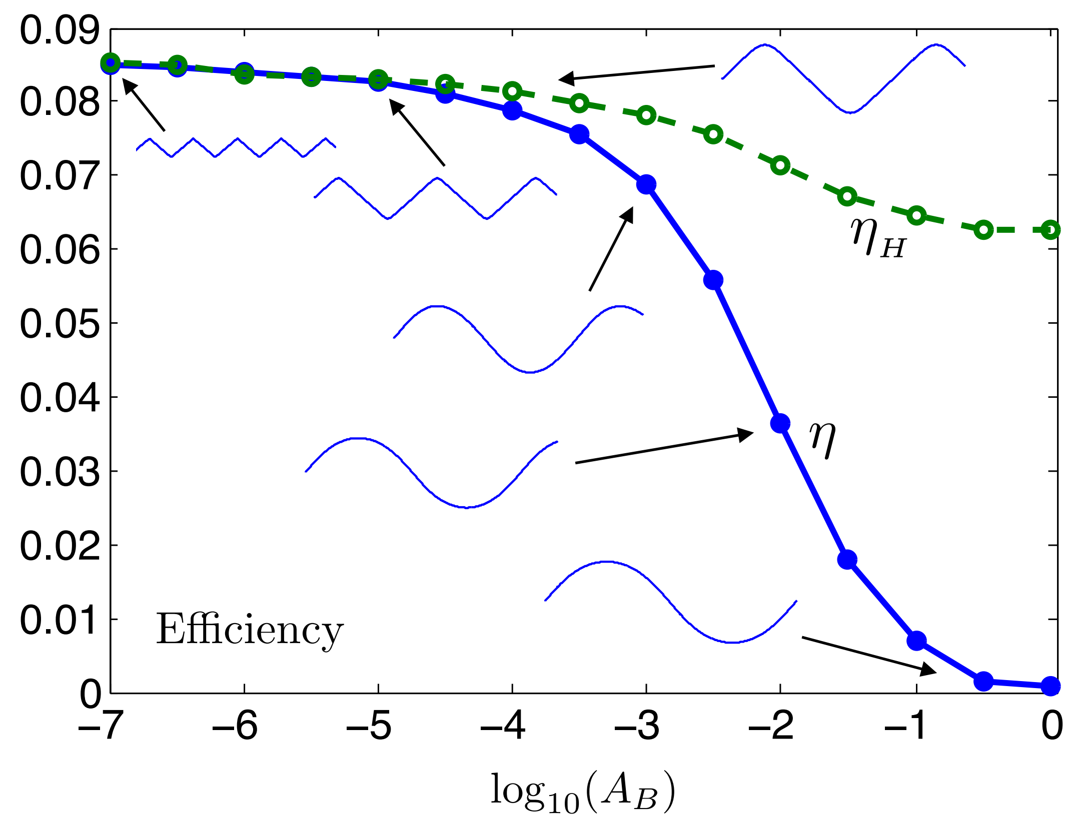
Figure 8. Oscillation frequency $\omega_c/2\pi$ at the bifurcation point

Shape matters: viscous dissipation vs bending costs

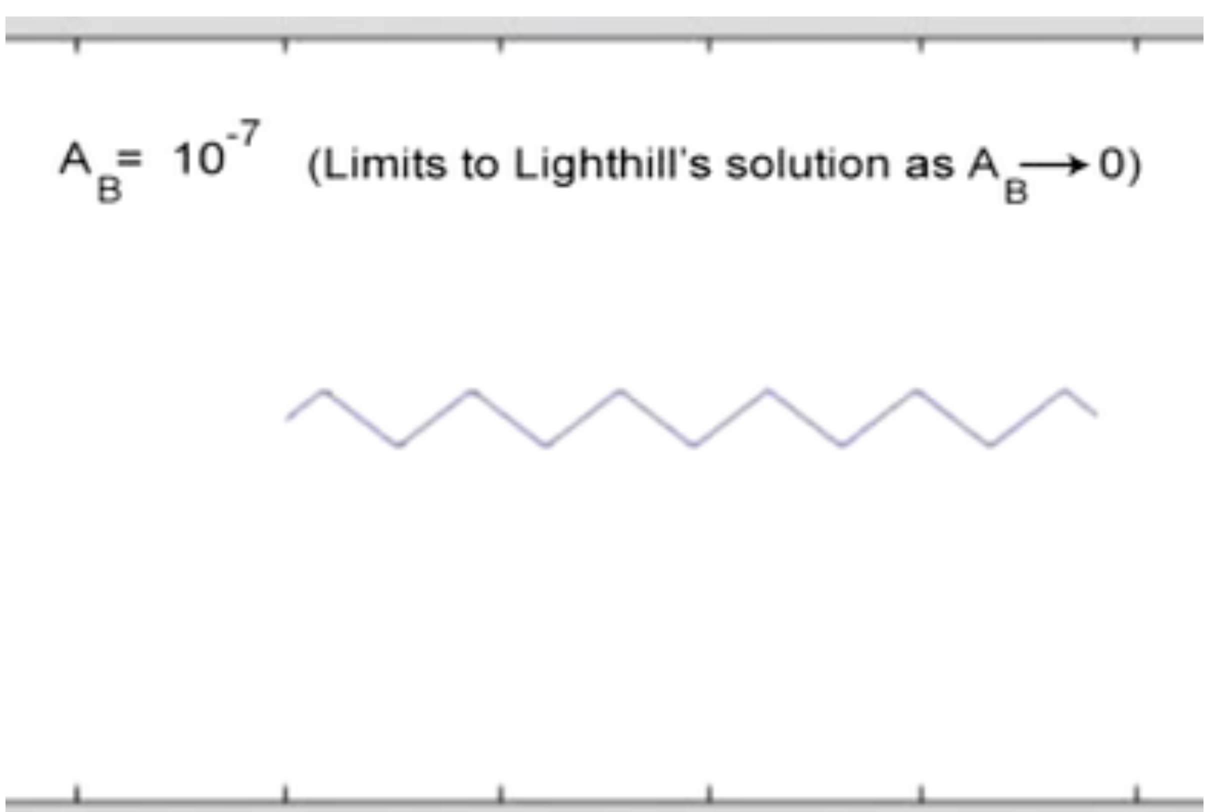
The “optimal” elastic flagellum:

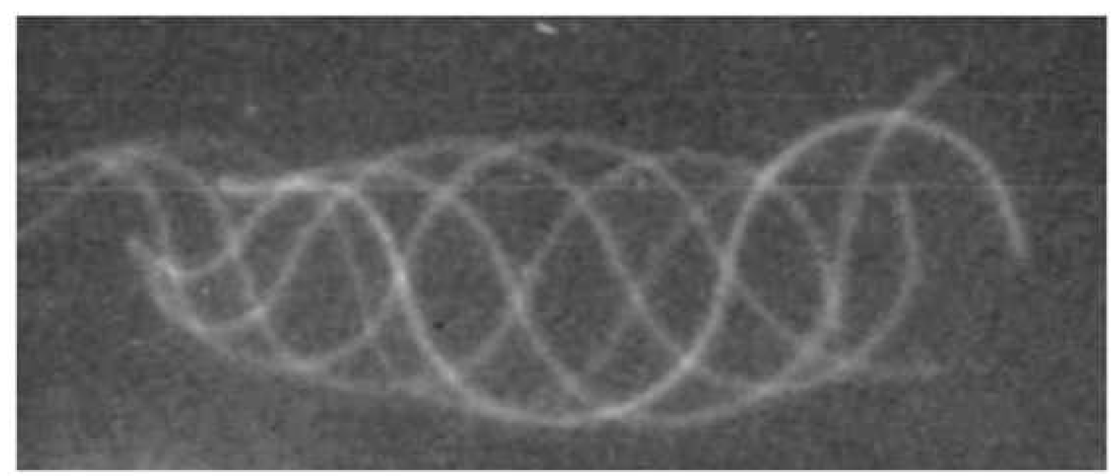


Lighthill (J.V. Neumann Lecture 1975)



A_B : Relative importance of bending costs

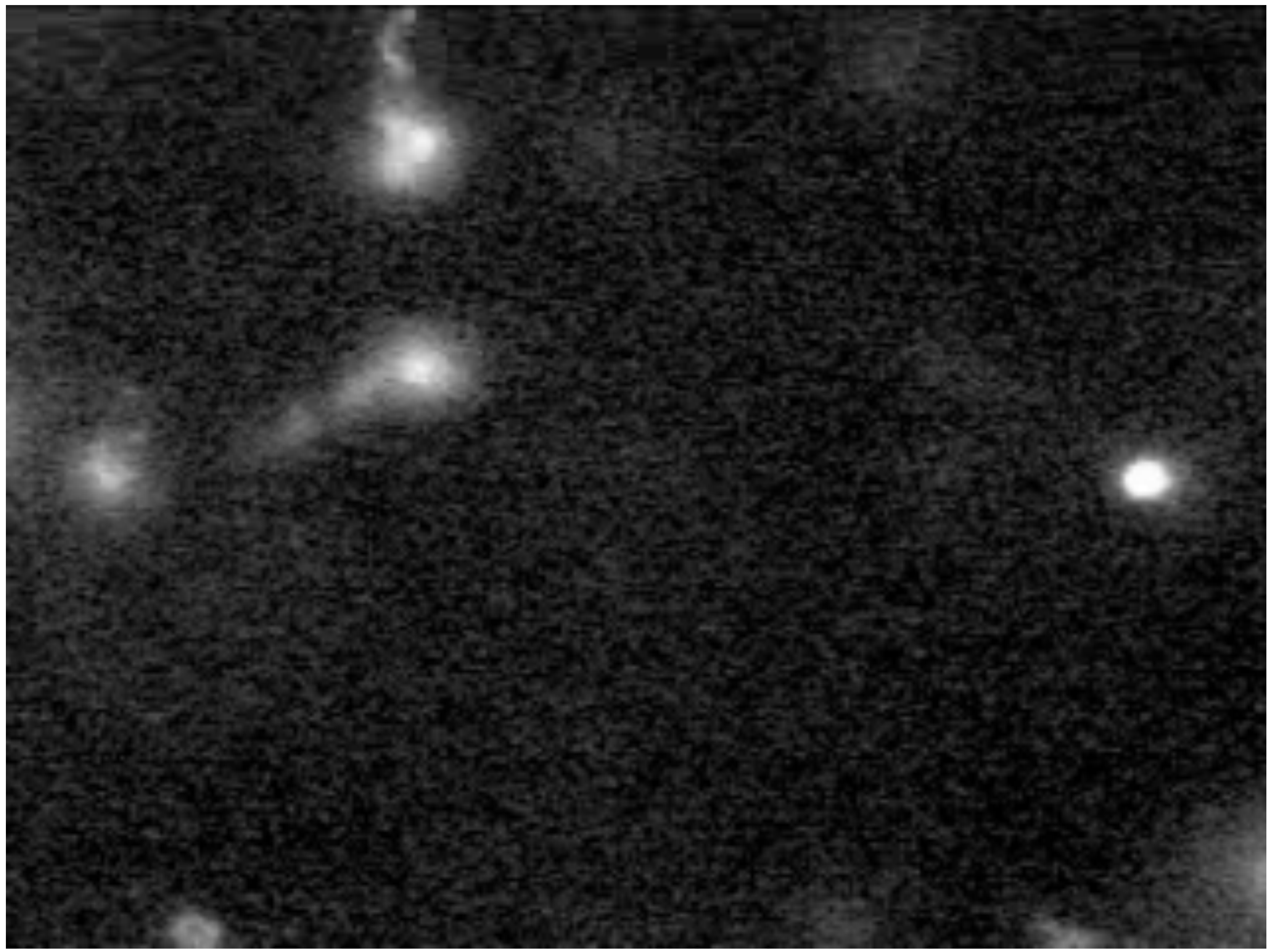




Spagnolie & Lauga, (Phys. Fluids 2009)

Most ***bacteria*** swim by rotating a slender, helical flagellum / many helical flagella.

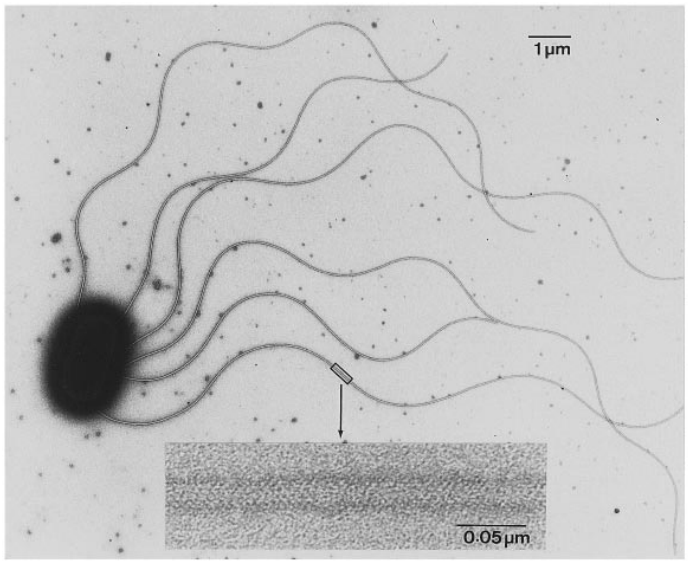
Helical waves (prokaryotic flagella): rotation of a solid helix leads to locomotion

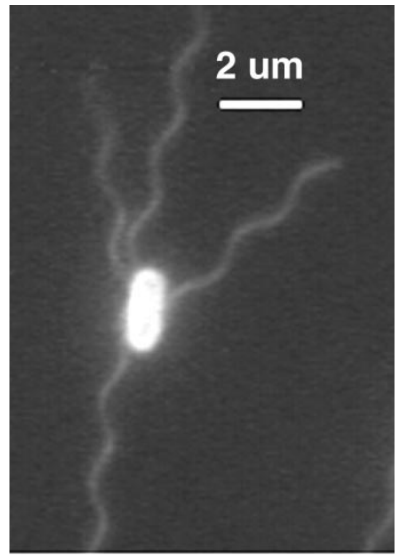


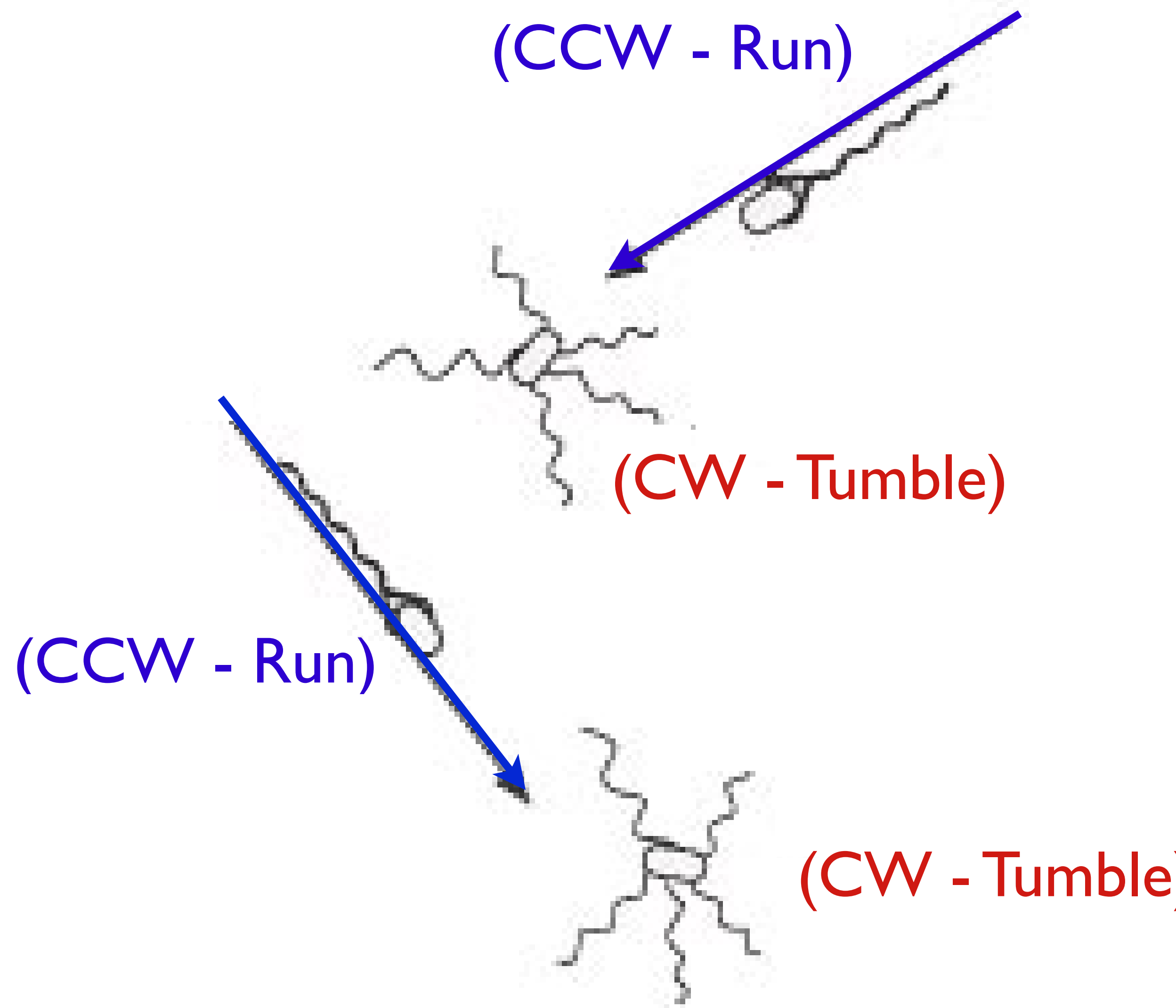
Rhodobacter sphaeroides
H. C. Berg, Harvard

Most ***bacteria*** swim by rotating a slender, helical flagellum / many helical flagella.

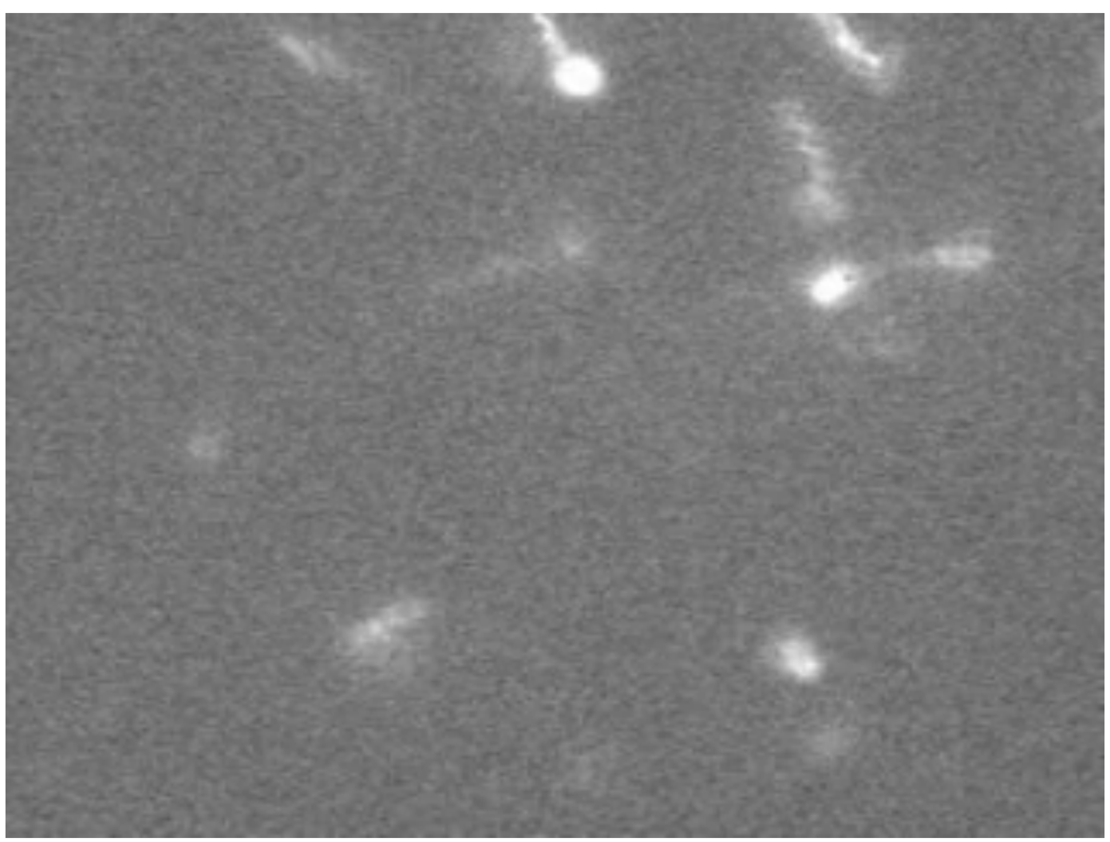
Salmonella and *E. coli* are “peritrichous” (many flagella)...







...and exhibit ***run*** and ***tumble*** locomotion:

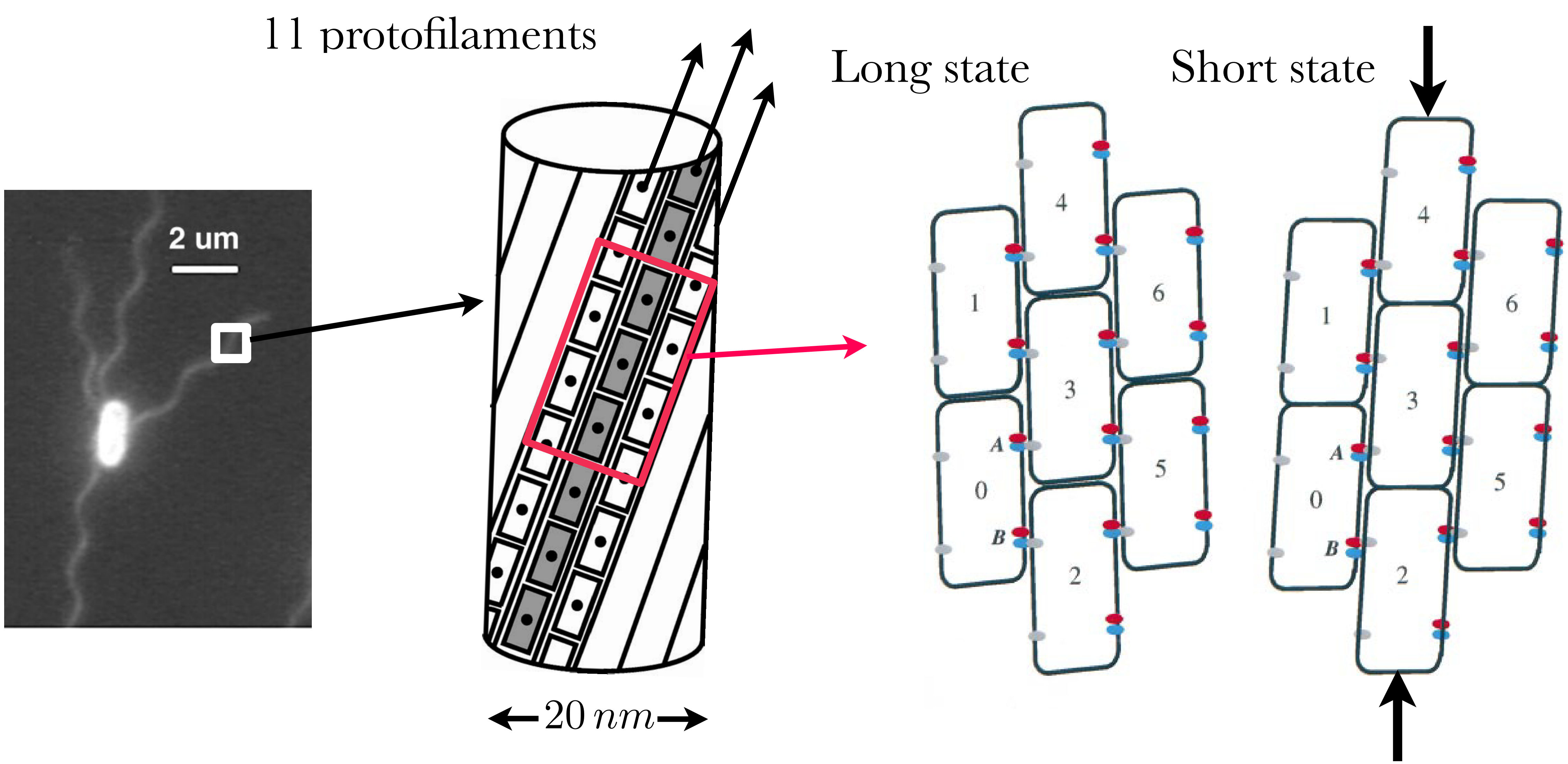


Berg Lab, Harvard

Namba & Vonderviszt, Quart. Rev. Biophys. (1997)
Turner, Ryu & Berg, J. Bacteriol. (2000)

But keep an eye on reality! For instance, CW and CCW rotations yield different behavior

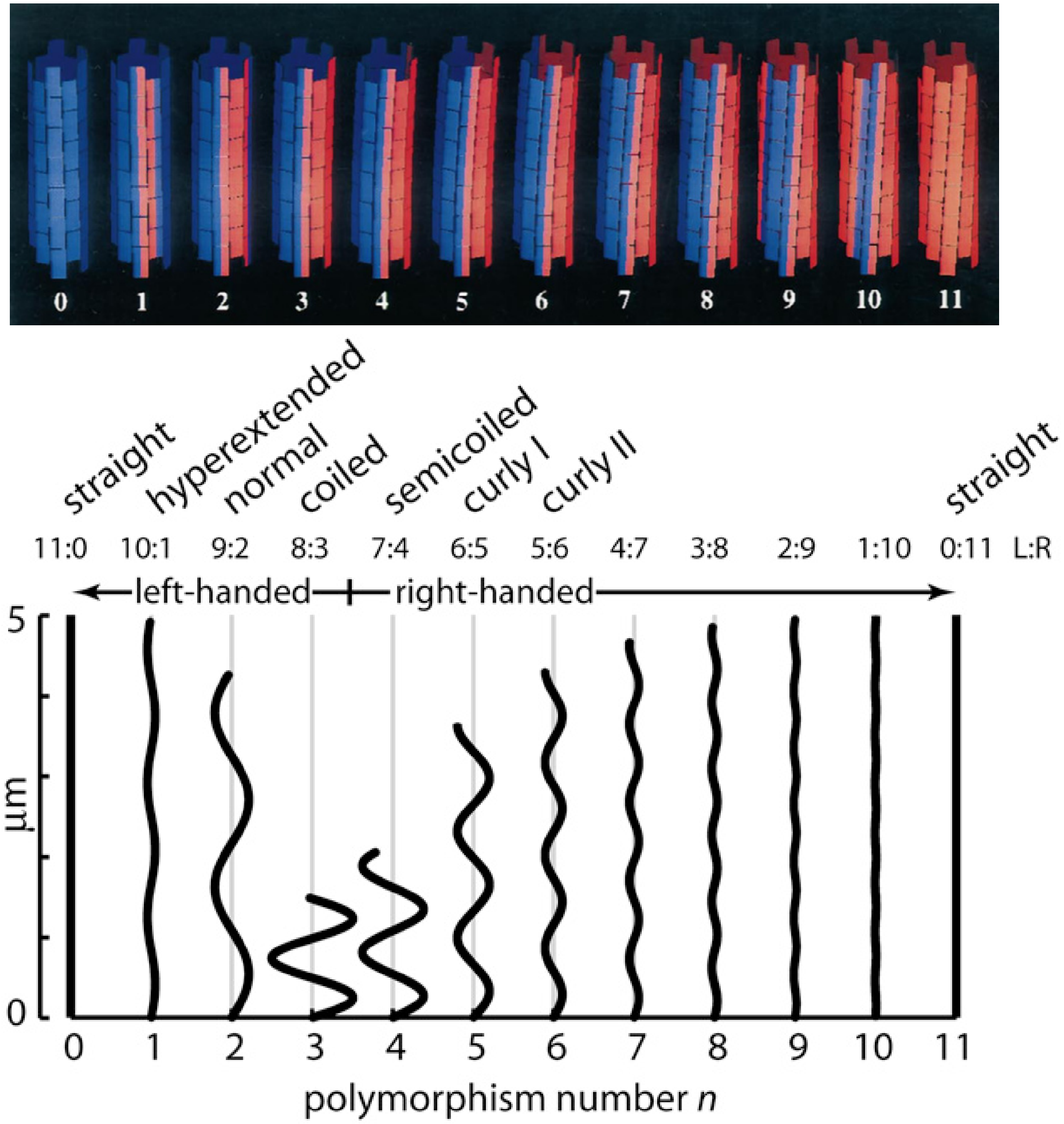
Polymerized Flagellin protein micro-structure is not symmetric...

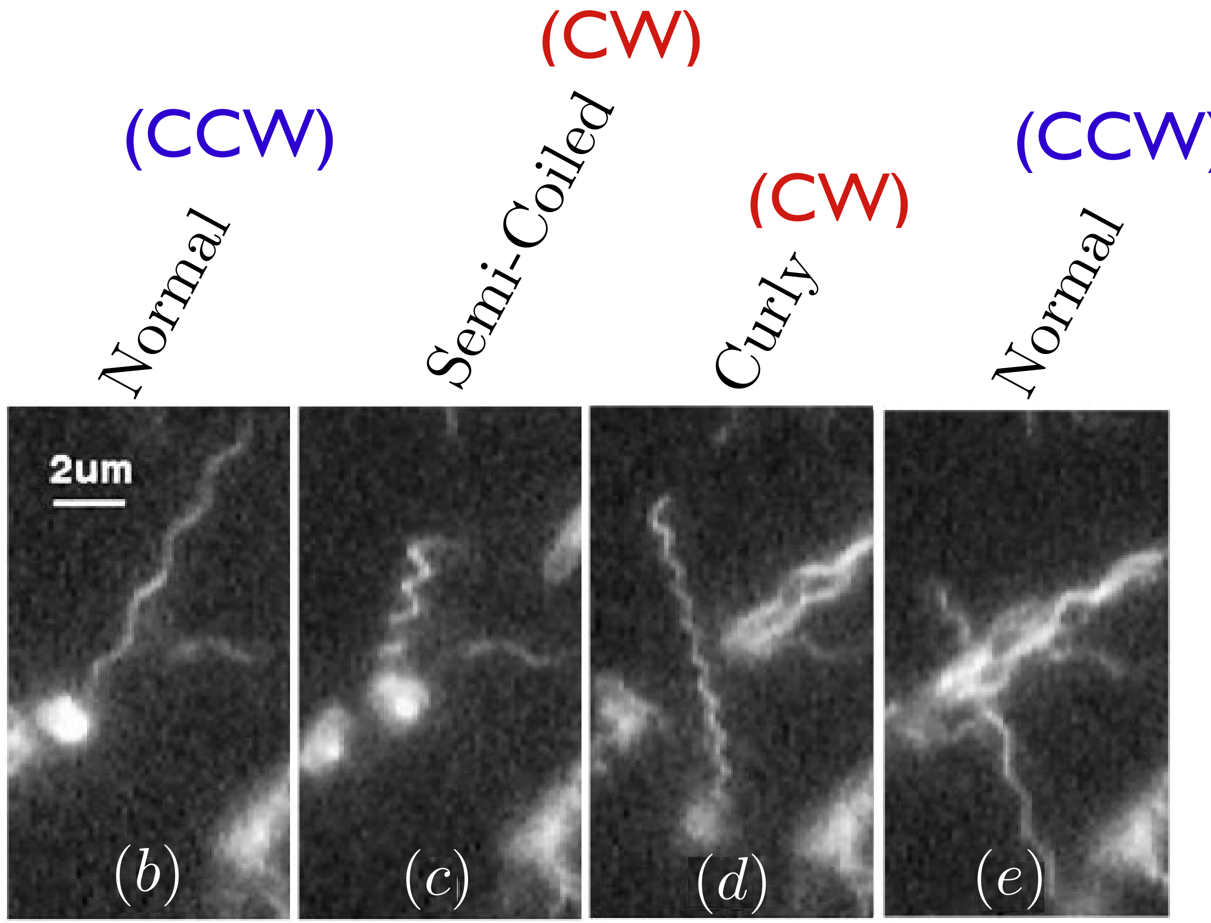


Asakura, Adv. Biophys. (1970)
Calladine, J. Mol. Biol. (1978)
Hasegawa et al., Biophys. J. (1998)
Srigiriraju & Powers, Phys. Rev. E (2006)

...leading to macroscopic curvature to balance the local twisting moments, and *12 distinct macroscopic waveforms* ("polymorphism").

Theoretical waveforms



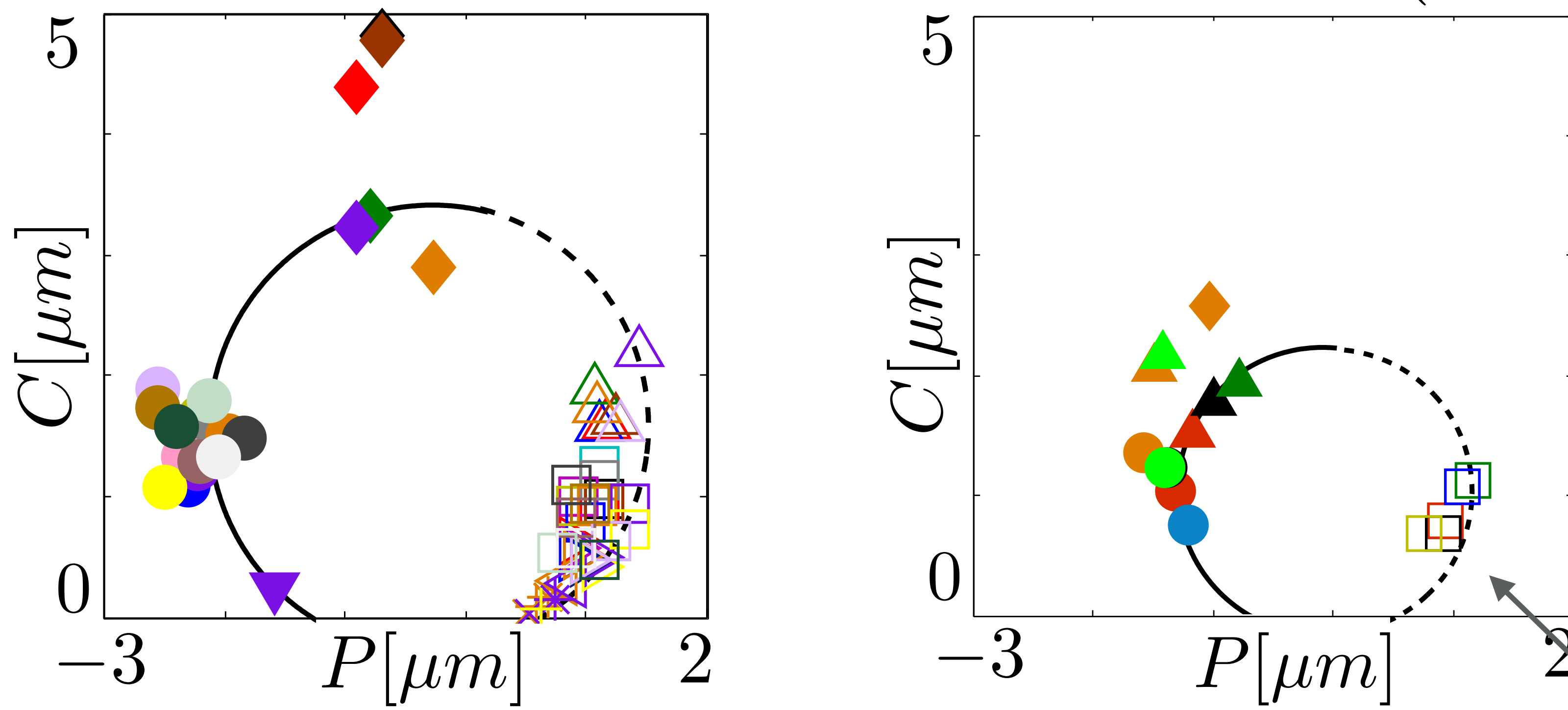


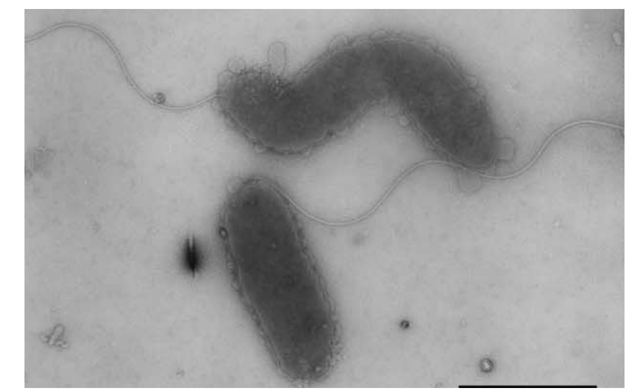
Turner, Ryu & Berg, J. Bacteriol. (2000).

Asakura, Adv. Biophys. (1970)
Calladine, J. Mol. Biol. (1978)
Hasegawa et al., Biophys. J. (1998)
Srigiriraju & Powers, Phys. Rev. E (2006)
Darnton & Berg, Biophys. J. (2007)

Experimental observations indicate a circular relationship in the pitch-circumference plane

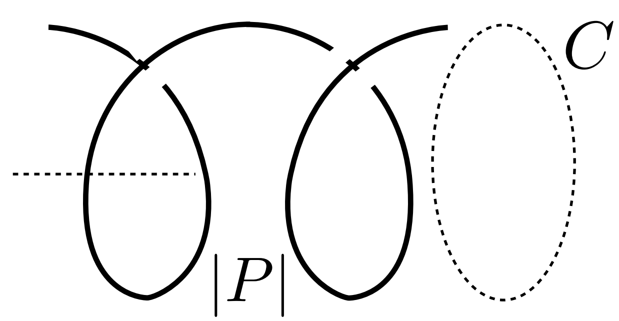
Peritrichous   Monotrichous (Polar)

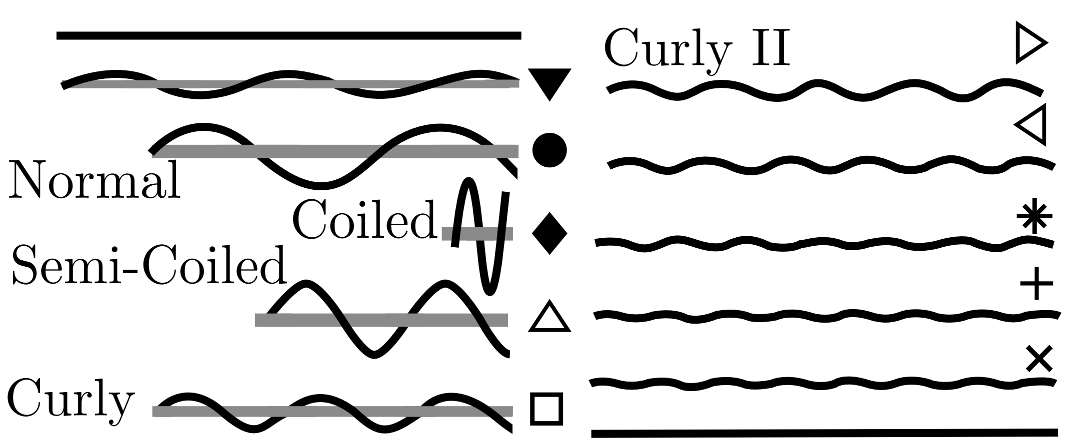




Idiomarina loihiensis

This curve helped identify a second protein (Flagellin-II) building block!





Shibata, Alam & Aizawa, J. Mol. Biol. (2005)
Fujii, Shibata, Aizawa, J. Mol. Biol. (2008)

Are biological fluids any different?

Biolocomotion in viscoelastic fluids

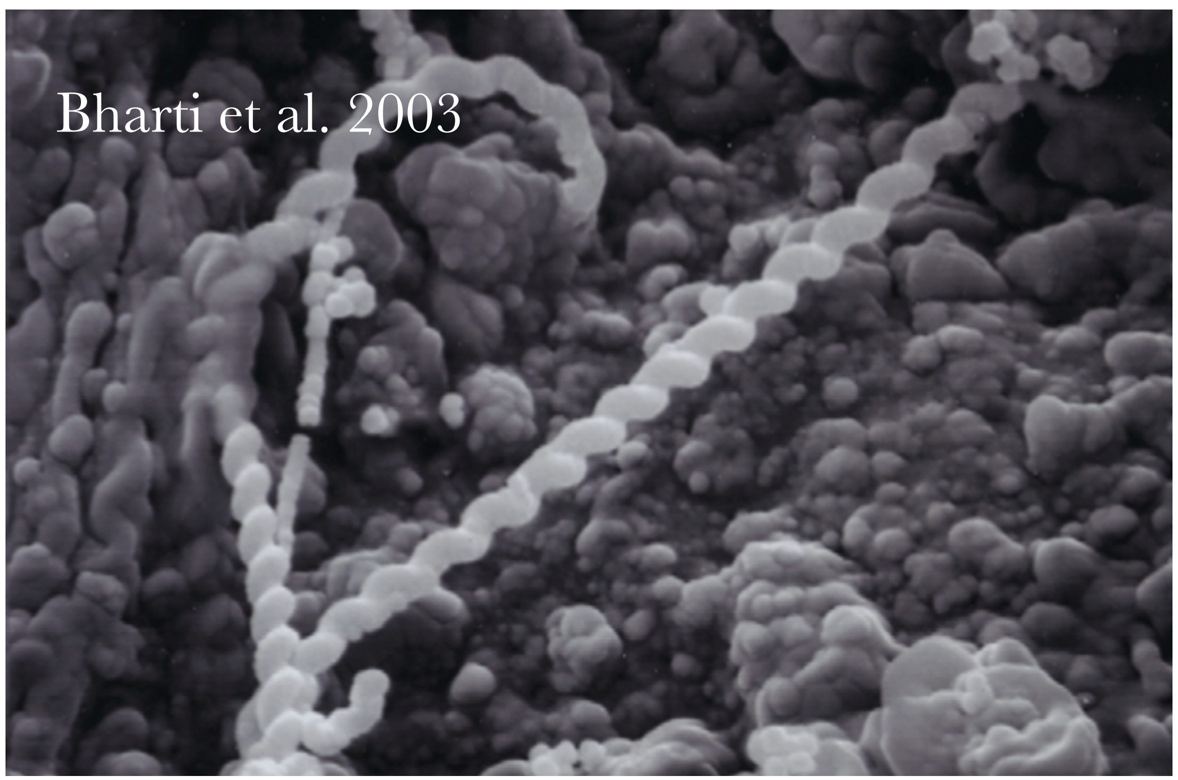
Biological fluids are often host to a polymeric microstructure

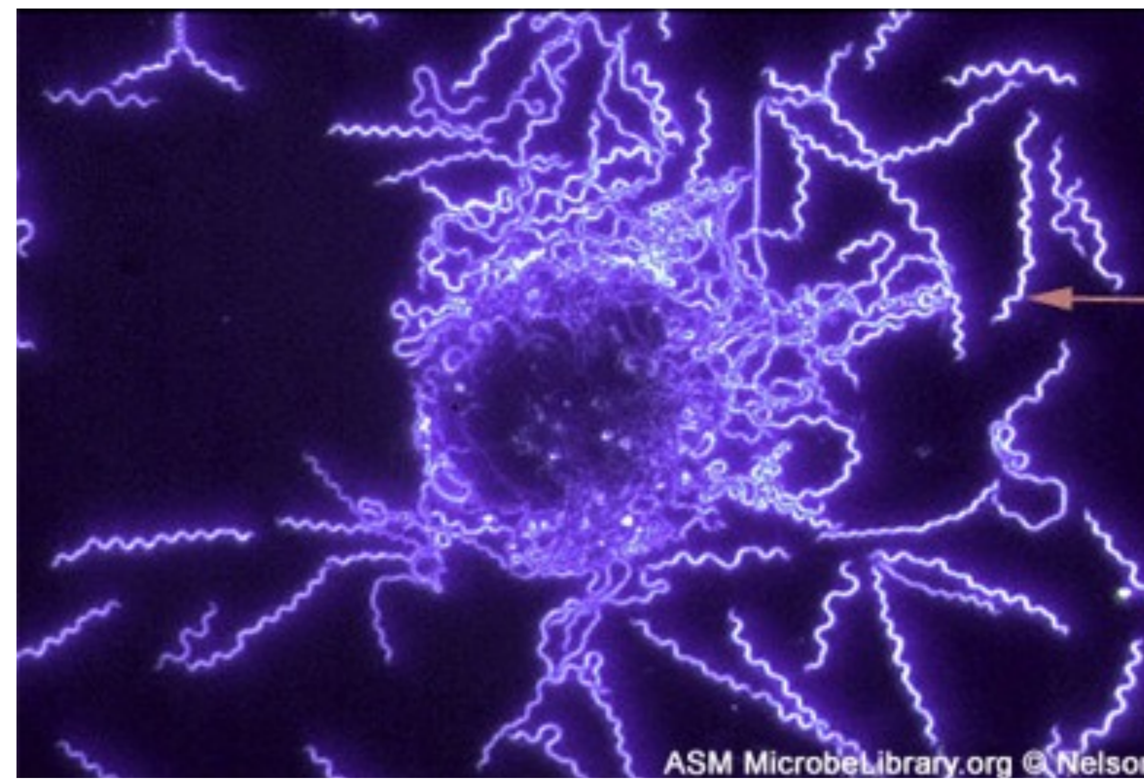
In flow: viscous stresses compete with entropic contraction of polymers

Helical bacteria

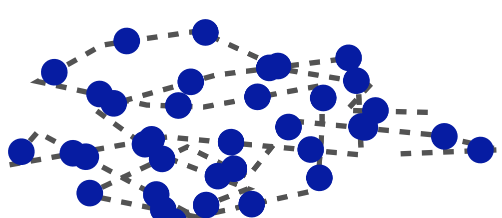
Leptospira (Leptosprosis) and *B. burgdorferi (Lyme disease)*

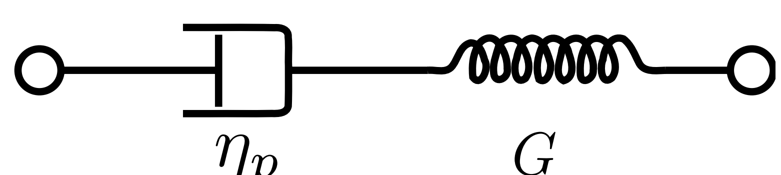
swim faster...





Berg & Turner, 1979; Spielman & Kimsey, 1990





$$\lambda_1 = \frac{\eta_p}{G}$$

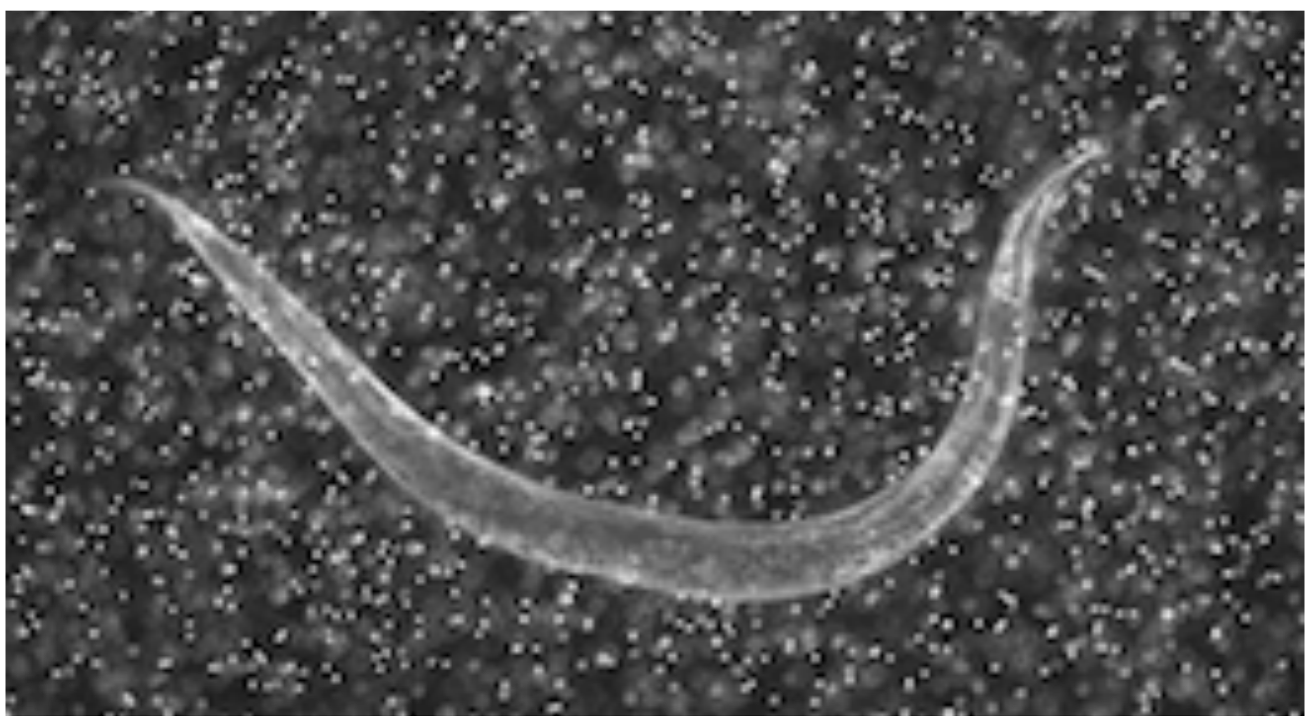
Relaxation time

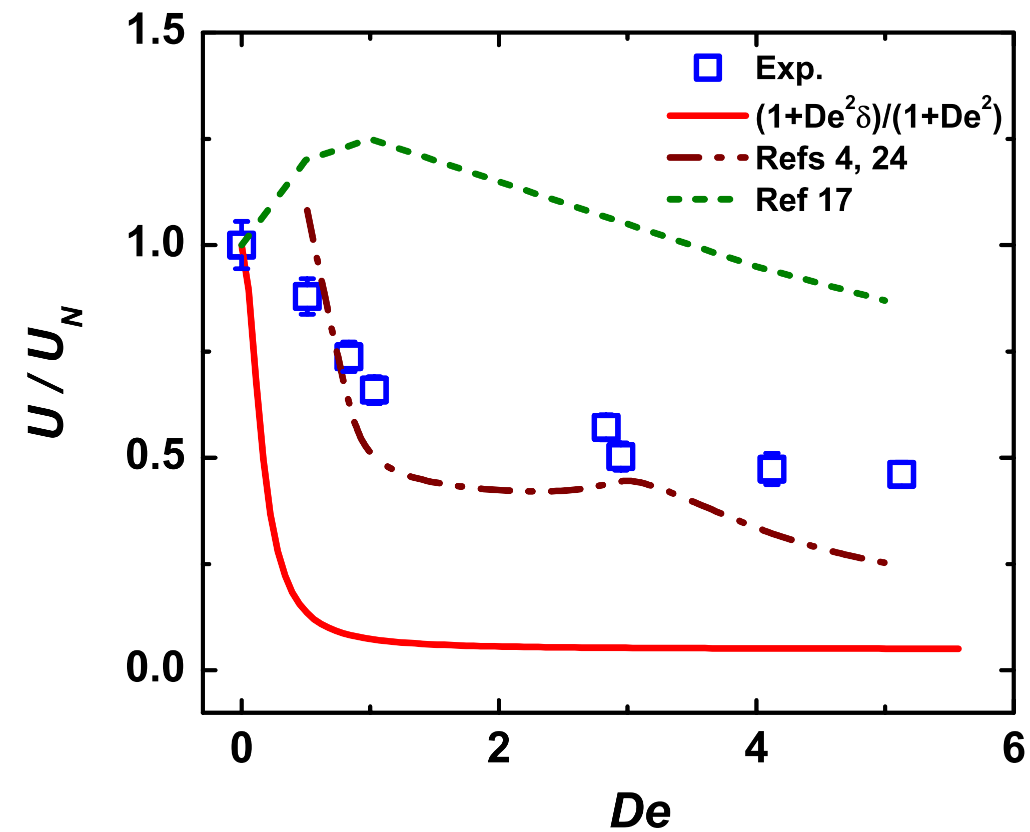
Biolocomotion in viscoelastic fluids

Biological fluids are often host to a polymeric microstructure

In flow: viscous stresses compete with entropic contraction of polymers

...while *C. elegans* swims slower...





Lauga, *Phys. Fluids*, 2007
Teran, Fauci & Shelley, *Phys. Rev. Lett.*, 2010
Shen & Arratia, *Phys. Rev. Lett.*, 2011

A new dimensionless number appears:

$$\text{Deborah number: } \mathrm{De} = \lambda_1 \omega$$

Free historical notes:

Proposed by Markus Reiner (Technion) (1920):

"The mountains flowed before the Lord" (Deborah; Judges 5:5)

Also coined the term: "rheology" w/ Bingham (study of deformation/flow of matter)

Inspired by the *aphorism of Simplicius:* "panta rhei" (*Everything flows*)

What tools do we have?

Linear PDEs
Green's functions
Moment expansion / method of reflections / method of images
Boundary integral representation
Slender body theory
…

What tools do we have?

~~Linear PDEs~~
~~Green's functions~~
~~Moment expansion / method of reflections / method of images~~
~~Boundary integral representation~~
~~Slender body theory~~
~~…~~

Fluid memory… and worse
Coupled nonlinear time-dependent PDEs… with moving immersed boundaries!
e.g. Stokes/Oldroyd-B:

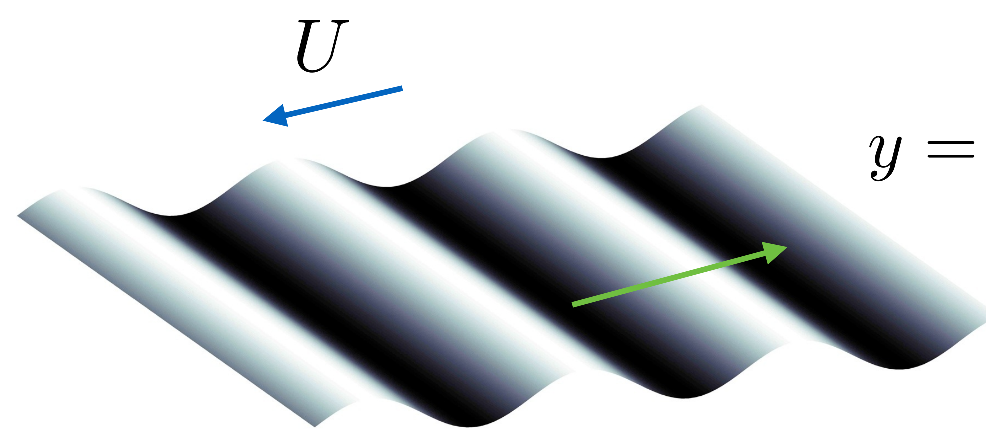
$$\nabla p = \eta_s \nabla^2 \mathbf{v} + \nabla \cdot \boldsymbol{\tau}^p \qquad \nabla \cdot \mathbf{v} = 0$$

$$\boldsymbol{\tau}^p + \lambda_1 \overset{\nabla}{\boldsymbol{\tau}}{}^p = \eta_p \dot{\boldsymbol{\gamma}} \qquad \overset{\nabla}{\boldsymbol{\tau}} = \frac{\partial \boldsymbol{\tau}}{\partial t} + \mathbf{u} \cdot \nabla \boldsymbol{\tau} - \boldsymbol{\tau} \cdot \nabla \mathbf{u} - \nabla \mathbf{u}^T \cdot \boldsymbol{\tau}$$

Separation of time-scales
Finite-time blow up, "high-Weissenberg number catastrophe", …

(i.e. Pray for a small parameter/symmetry *and* start computin')

Swimming of a 2D sheet in a viscoelastic fluid (Lauga, *Phys. Fluids*, 2007)

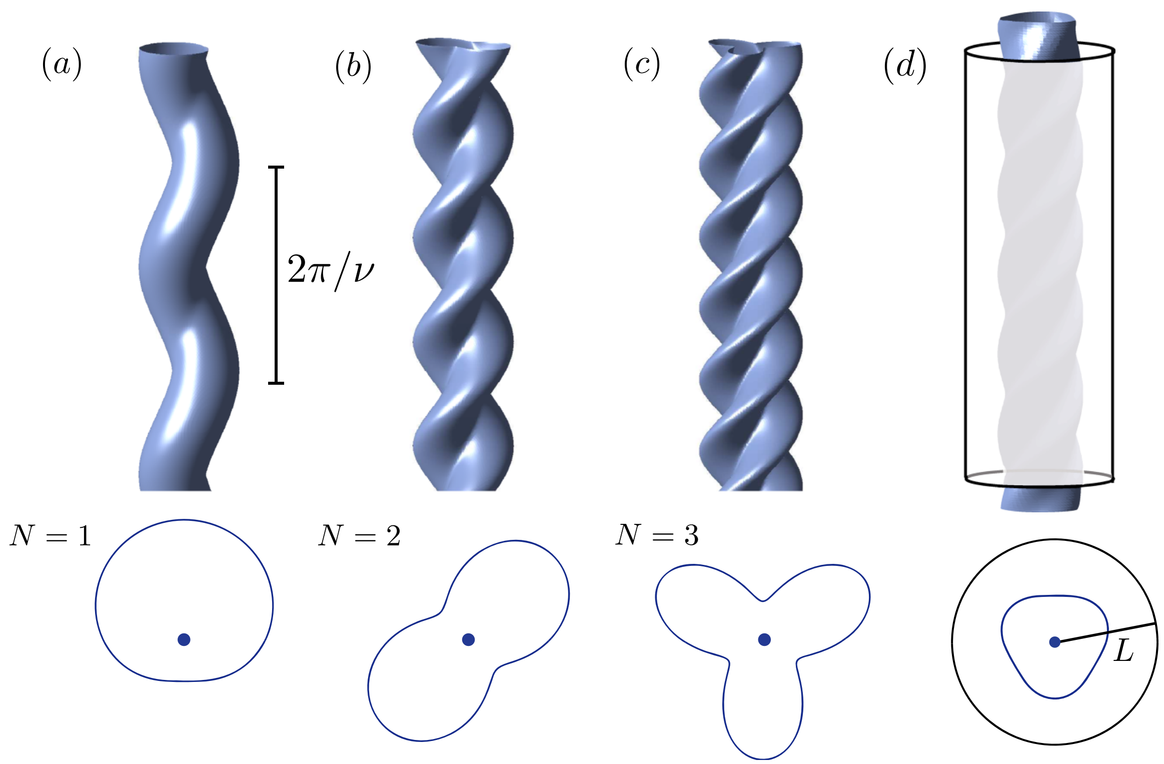


Stokes/Oldroyd-B: $\nabla p = \nabla \cdot \boldsymbol{\tau}$, $\nabla \cdot \mathbf{v} = 0$ $\quad \boldsymbol{\tau} = \boldsymbol{\tau}_0 + \epsilon \boldsymbol{\tau}_1 + \ldots$

Small-amplitude asymptotics: $\boxed{\dfrac{U}{U_N} = \dfrac{1 + (\eta_s/\eta)De^2}{1 + De^2}}$ $\quad \mathrm{De} = \lambda_1 \omega$, $\eta = \eta_s + \eta_p$

Identical swimming speeds for: FENE-P, Johnson-Segalman-Oldroyd, Giesekus

Reciprocal theorem extensions (finite bodies, etc.): Elfring & Lauga, (2015) The results can be generalized for a wider class of helical bodies/waves



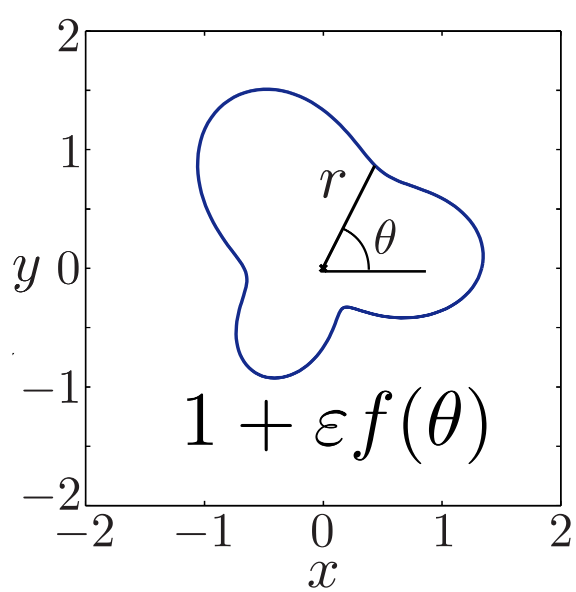
$$\boldsymbol{\tau}_1 + \frac{\mathrm{De}}{\nu}\left(\frac{\partial}{\partial\zeta} - \nu\frac{\partial}{\partial\theta}\right)\boldsymbol{\tau}_1 = \dot{\boldsymbol{\gamma}}_1 + \frac{\beta\,\mathrm{De}}{\nu}\left(\frac{\partial}{\partial\zeta} - \nu\frac{\partial}{\partial\theta}\right)\dot{\boldsymbol{\gamma}}_1$$

$$\dot{\boldsymbol{\gamma}}_\mathbf{1} = \sum_k \dot{\boldsymbol{\gamma}}_1^{(k)} \exp(ik\theta).$$

$$\boldsymbol{\tau}_\mathbf{1}^{(k)} = \eta^*(k)\dot{\boldsymbol{\gamma}}_1^{(k)}$$

complex viscosity $\eta^*(k) = (1 - ik\beta\,\mathrm{De})/(1 - ik\,\mathrm{De})$

$$\beta = \eta_s/\eta$$

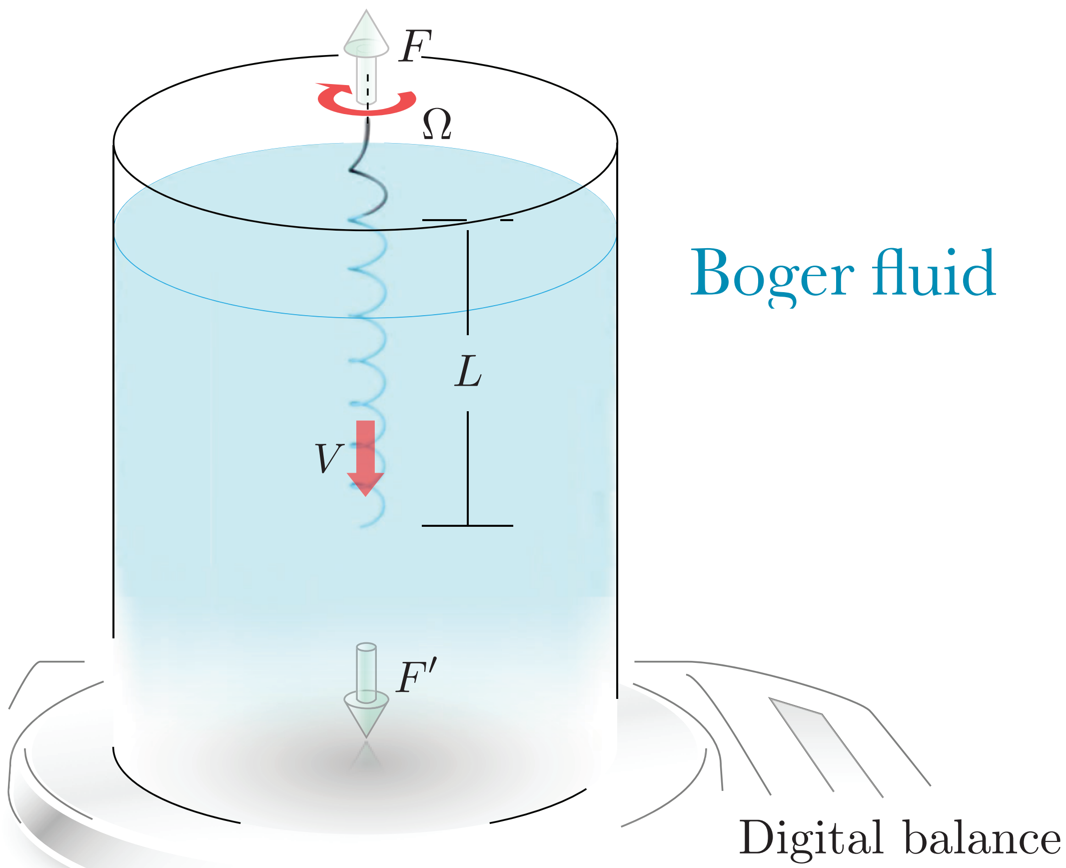


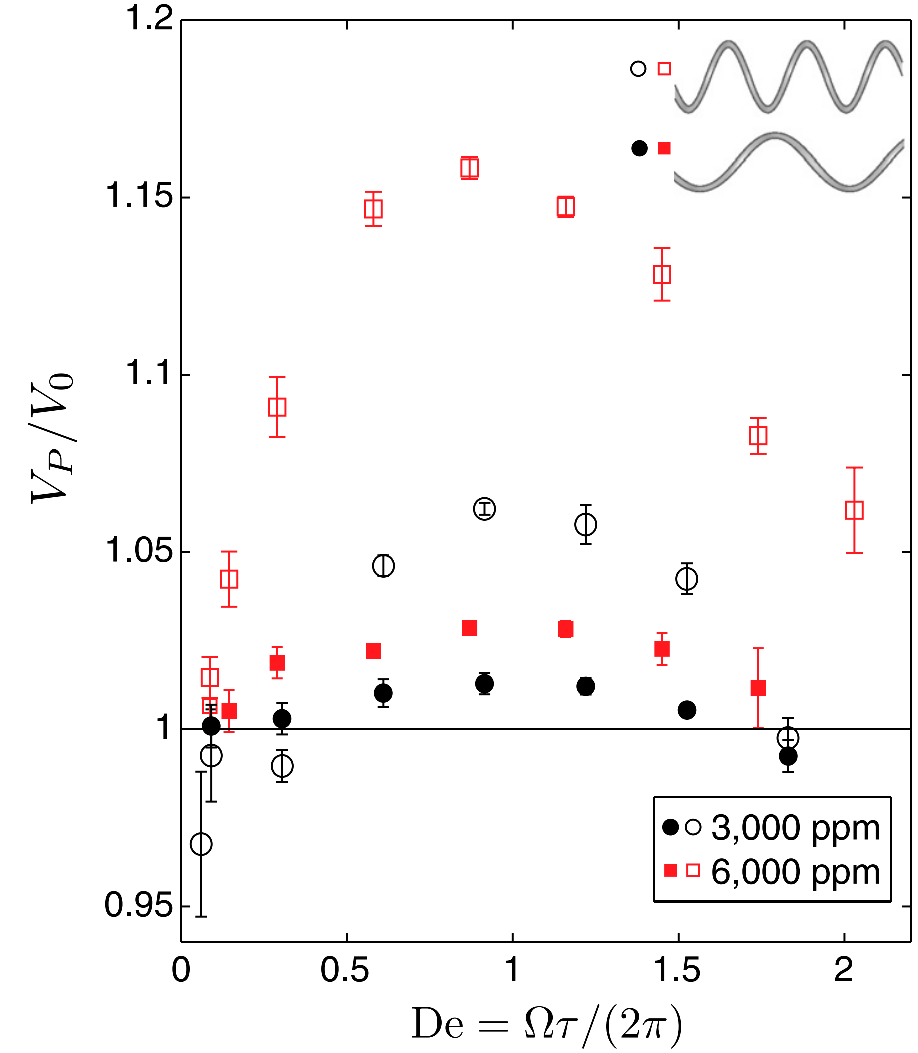
$$U = 2\varepsilon^2 \sum_{|k|\geq 1} \Re[\eta^*(k)]|\hat{f}_k|^2 J_k$$

Pumping is similar
Confinement is similar

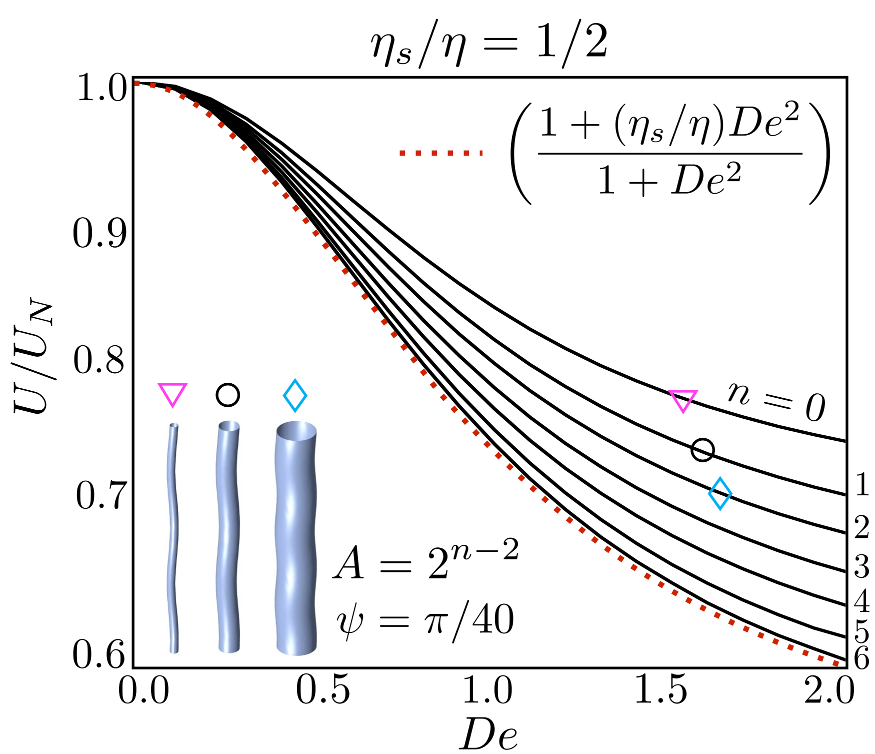
Lauga, *Phys. Fluids*, 2007,
Fu, Powers & Wolgemuth, *Phys. Rev. Lett.*, 2007
Leshansky, *Phys. Rev. E*, 2009
Fu, Wolgemuth & Powers, *Phys. Fluids*, 2009
Elfring, *Phys. Fluids*, 2015
Li & Spagnolie, *Phys. Fluids*, 2015

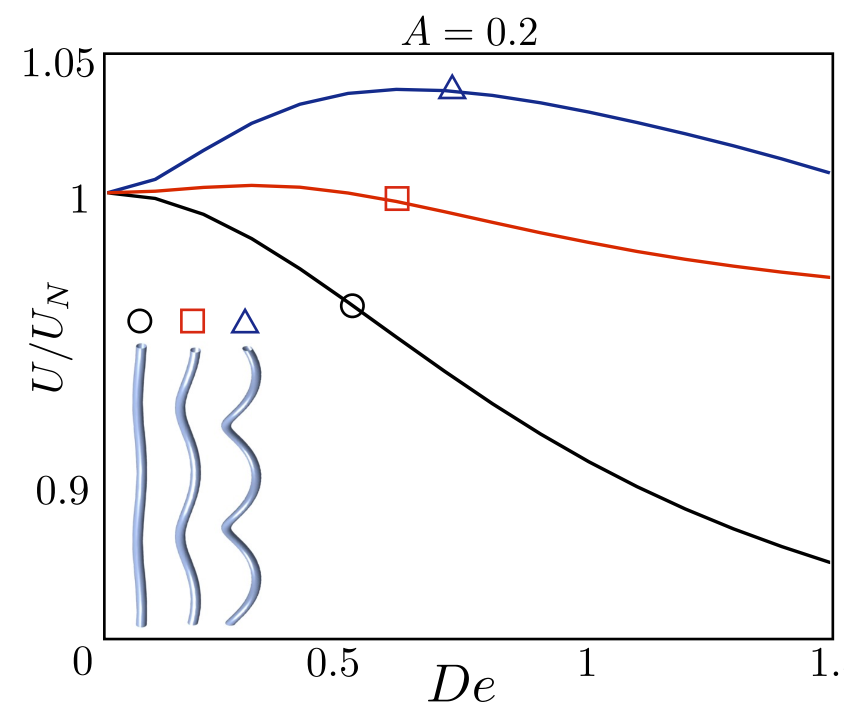
Enhanced swimming at large helical amplitudes

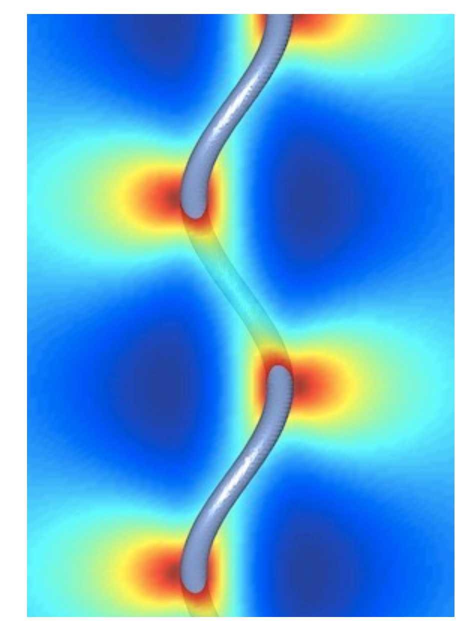




Stokes/
Oldroyd-B

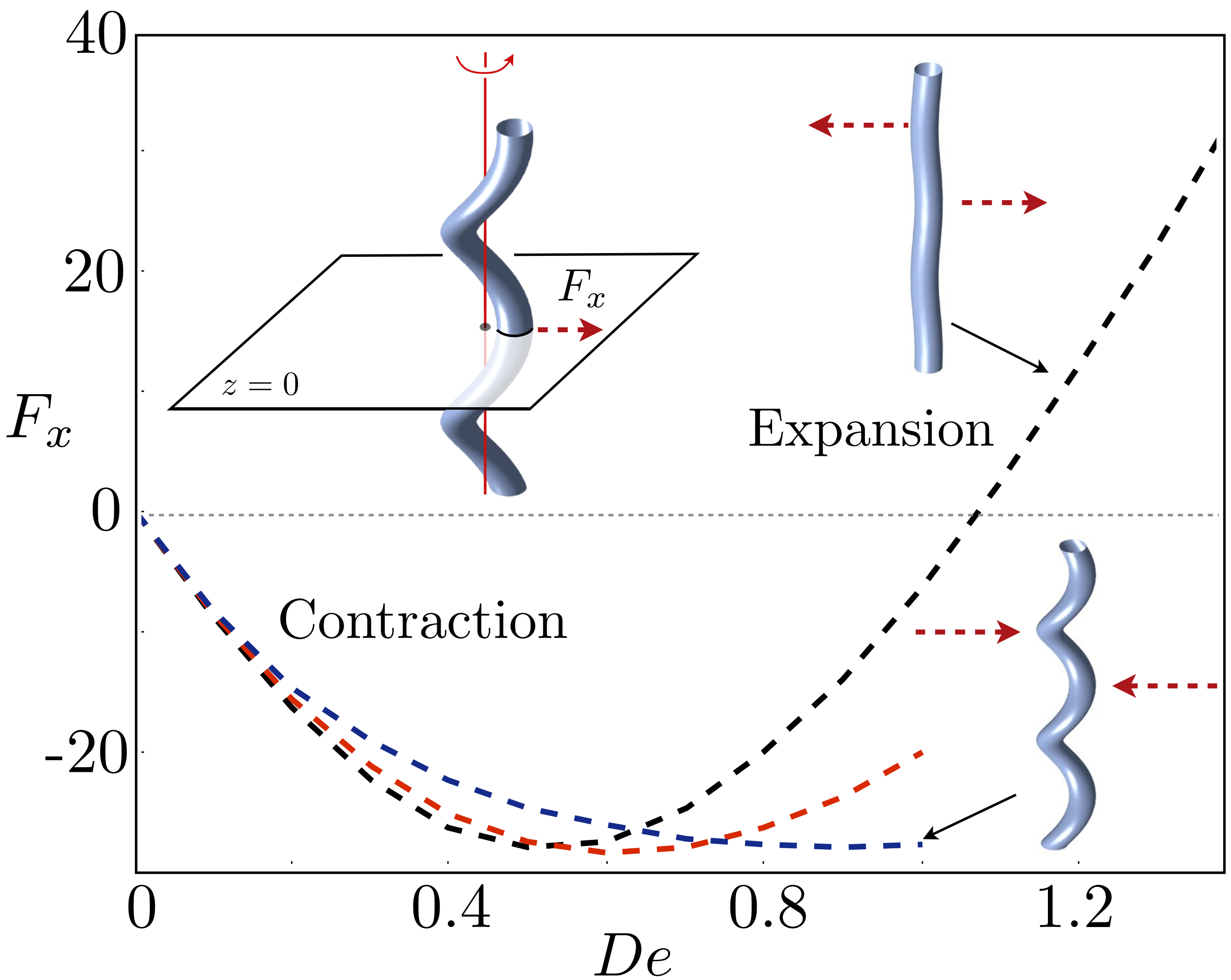


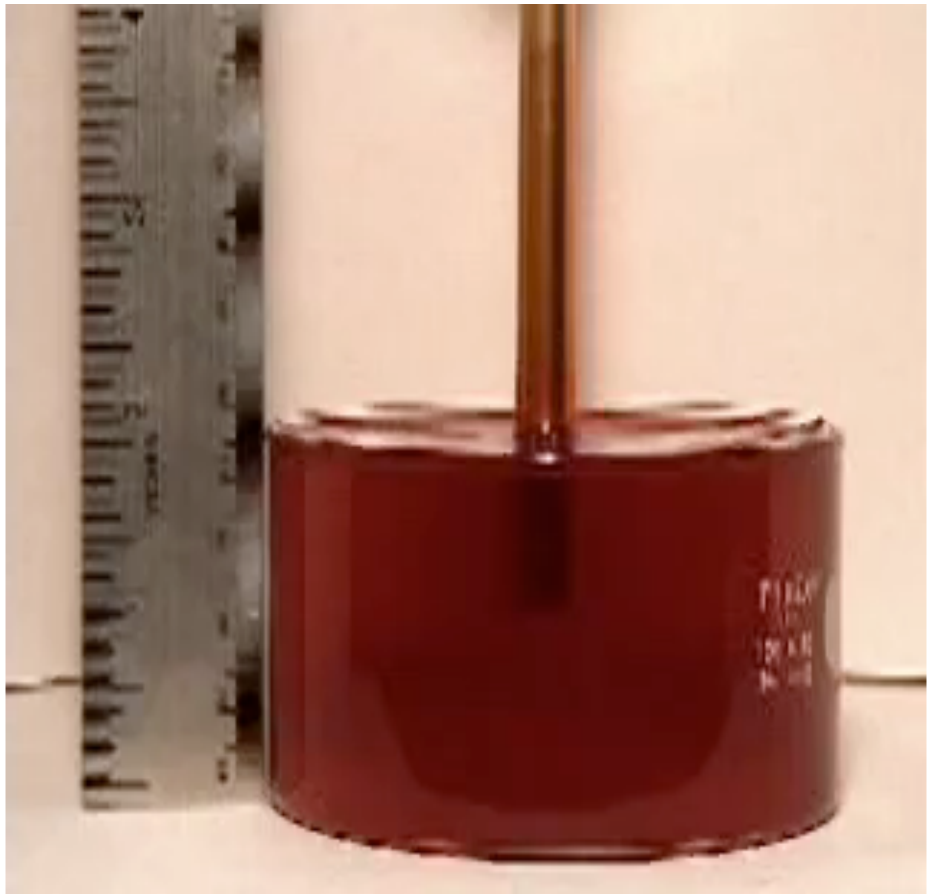




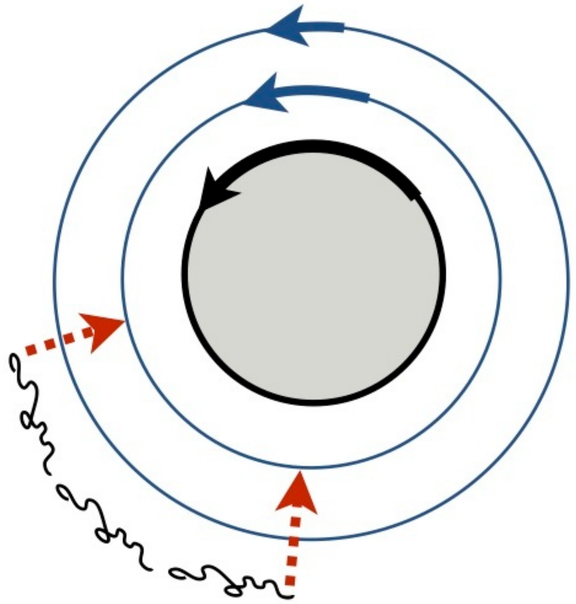
Liu, Powers & Breuer, *PNAS*, 2011
Spagnolie, Liu, & Powers, *Phys. Rev. Lett.*, 2013

Stability of flagellum geometry to hoop stress (strangulation effect)...



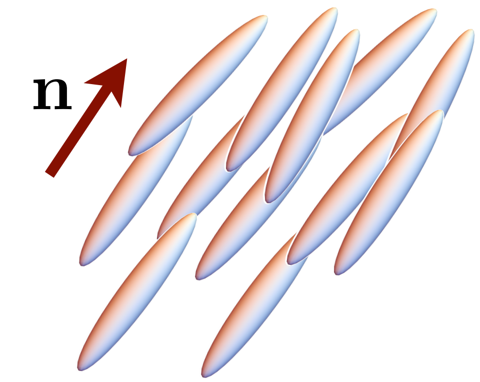


Rod-climbing (McKinley Lab, MIT)



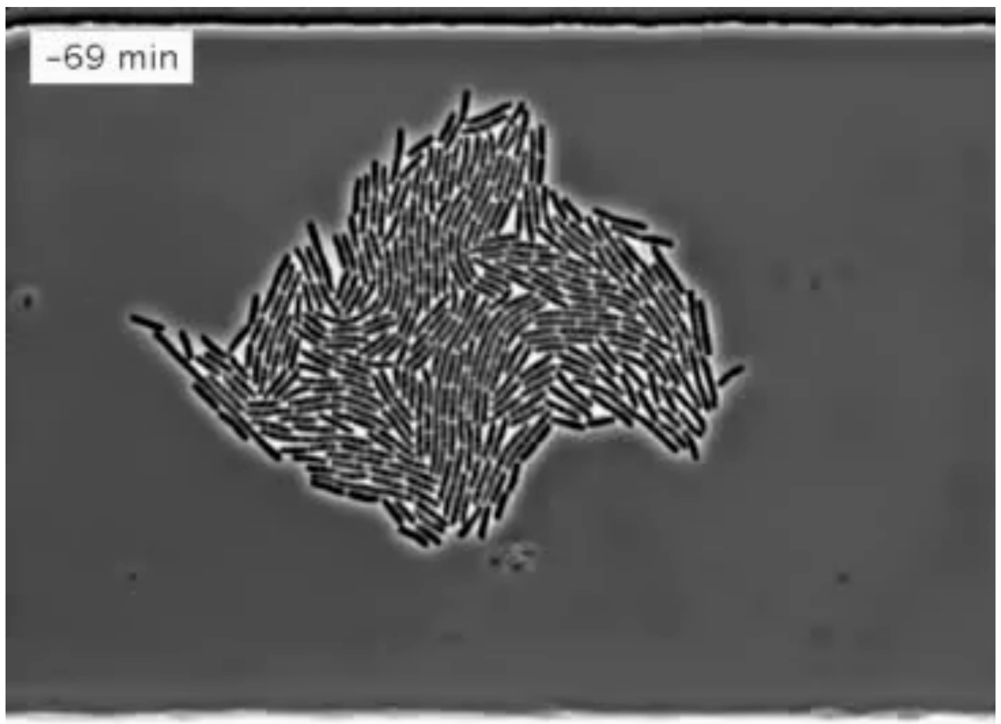
Flexible bodies? Multiple flagella?
"Active suspensions"? Shear-thinning?
Many questions remain open.

Yet other fluids are anisotropic (stress response is direction dependent)



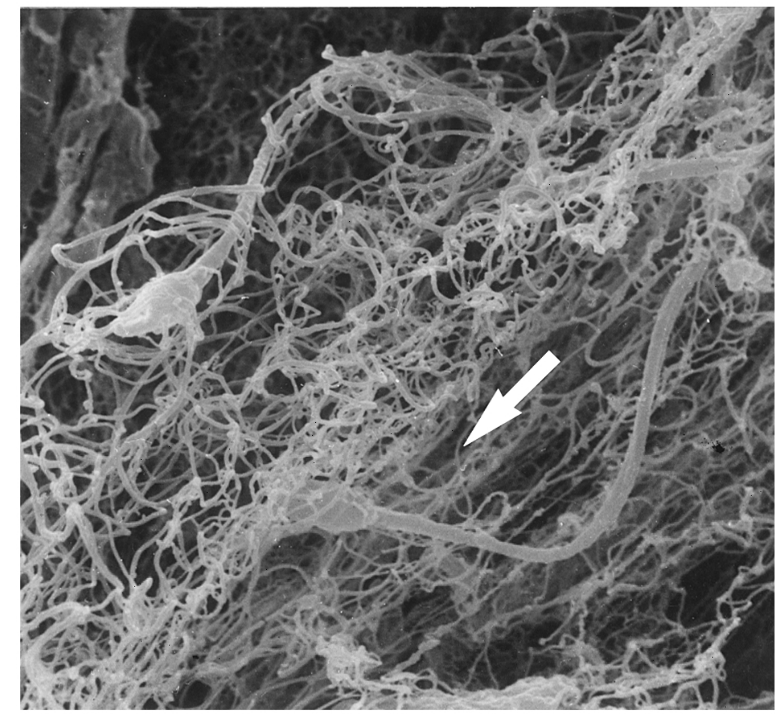
Mucus and biofilms are anisotropic
(in addition to viscoelastic, and shear-thinning…)

Biofilms

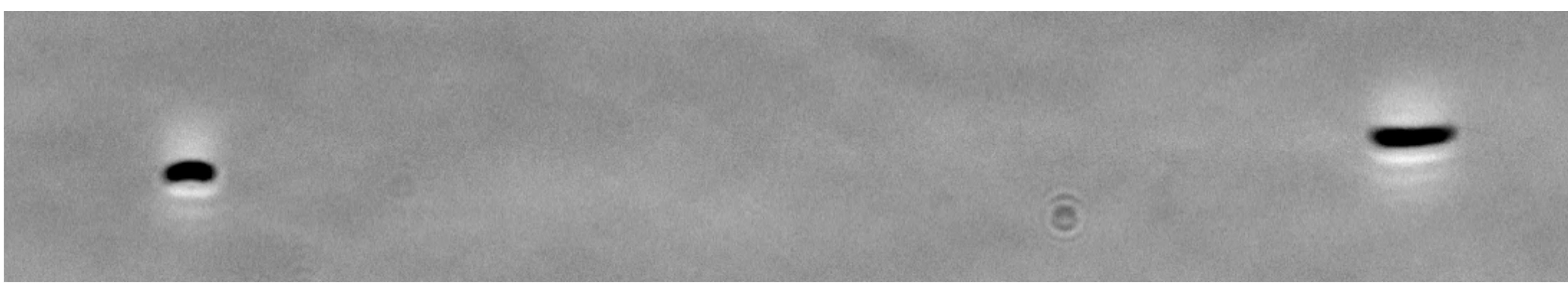


Boyer et al. Phys. Biol. (2011)

Cervical mucus



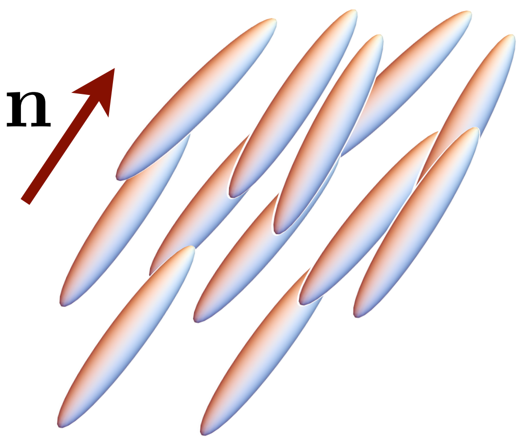
Chretien (2003)



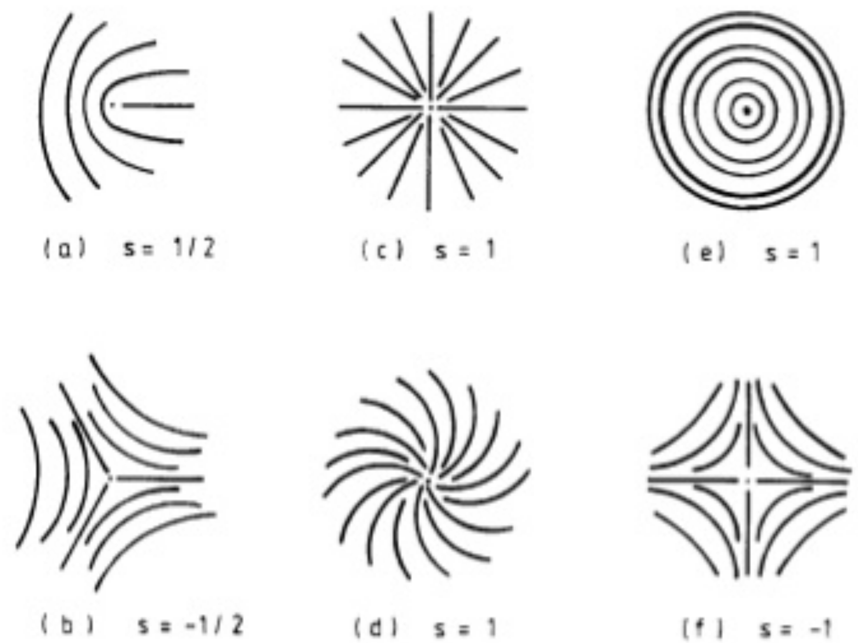
B. subtilis in a nematic liquid crystal (DSCG)

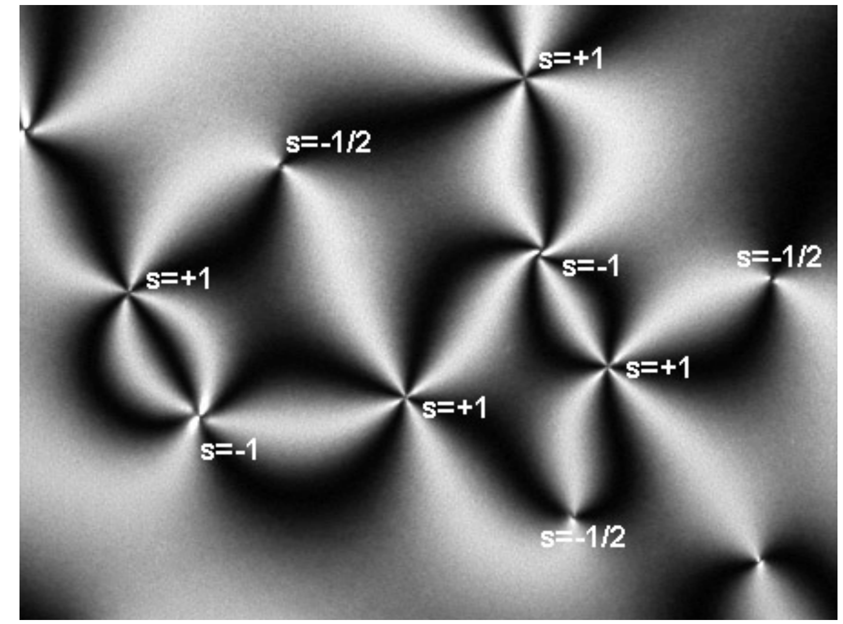
Mushenheim, Trivedi, Tuson, Weibel and Abbott, *Soft Matter*, 2014.

A nematic liquid crystal is a phase with **orientational order** but no positional order



Topological defects





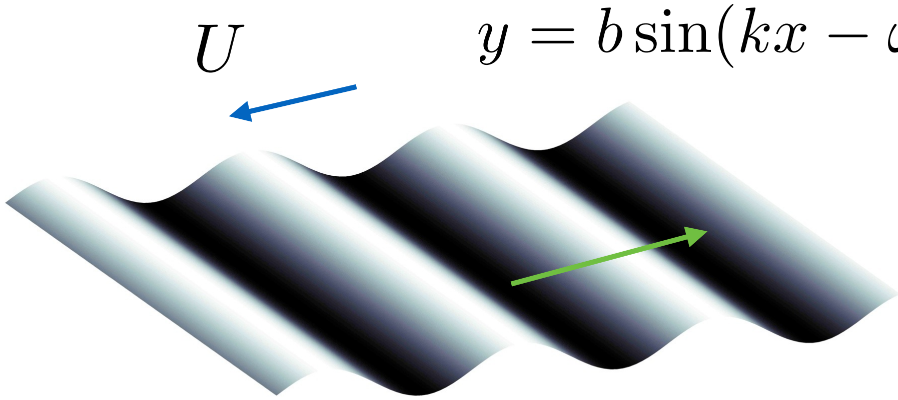
Deviations from uniform alignment result in an **elastic** response…

$$F(\hat{\mathbf{n}}) = \frac{K_1}{2}(\nabla \cdot \hat{\mathbf{n}})^2 + \frac{K_2}{2}(\hat{\mathbf{n}} \cdot \nabla \times \hat{\mathbf{n}})^2 + \frac{K_3}{2}[\hat{\mathbf{n}} \times (\nabla \times \hat{\mathbf{n}})]^2,$$

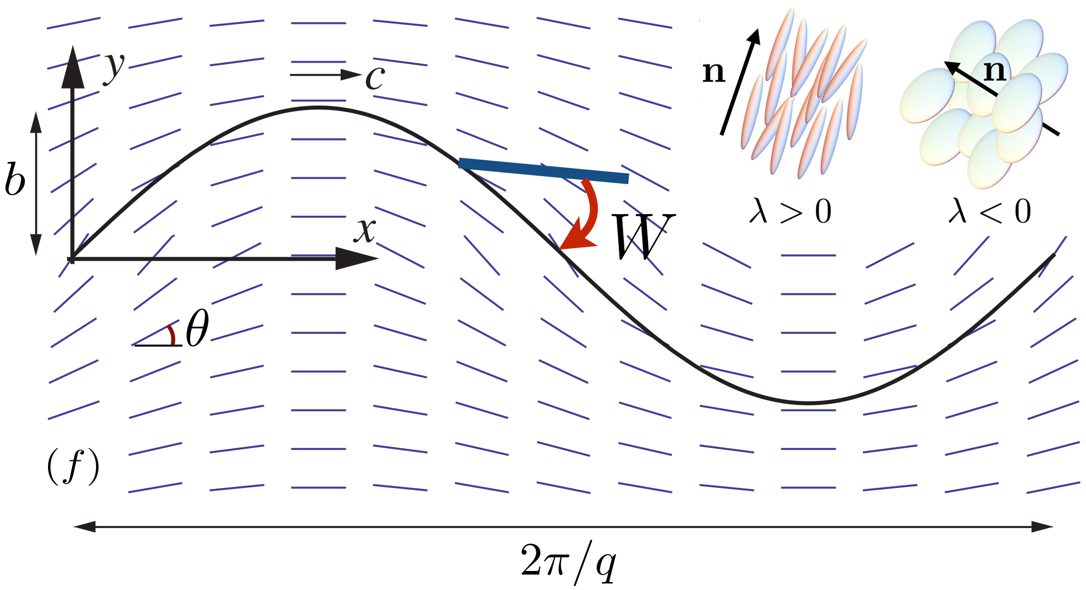
Splay Twist Bend

e.g. in 2D, $\mathbf{H} = -\dfrac{\delta \mathbf{F}}{\delta \mathbf{n}(\theta)} = (\nabla^2\theta)\mathbf{n}$

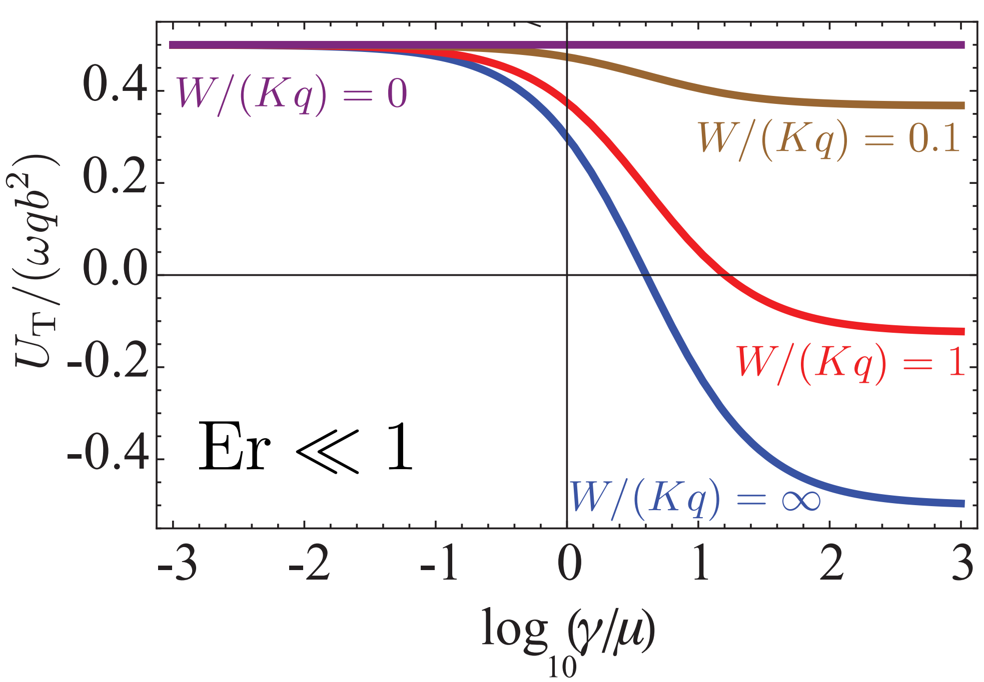
“Taylor’s swimming sheet” in a nematic liquid crystal

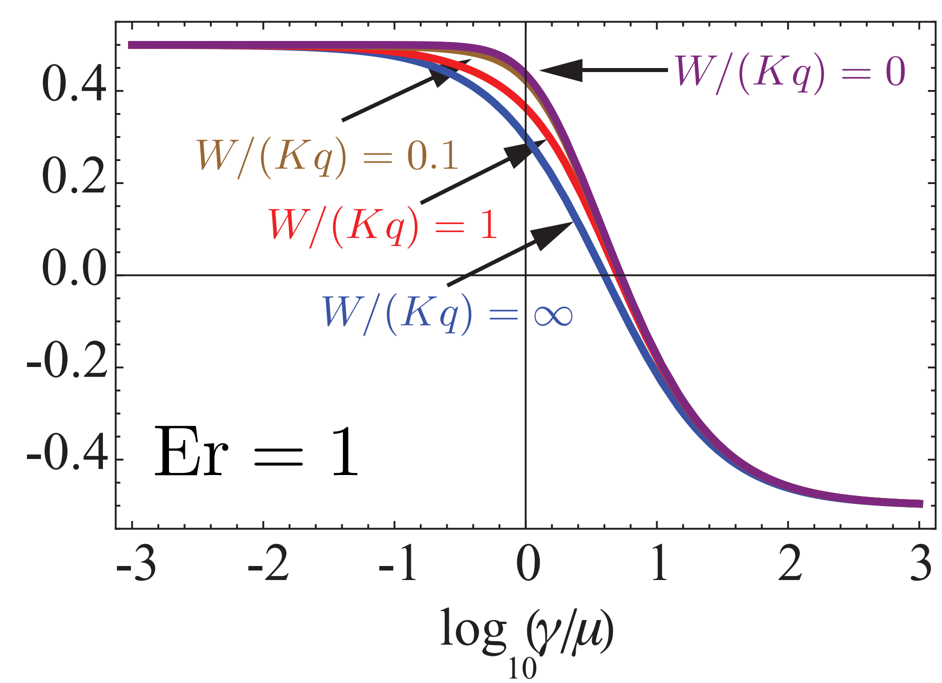


$$y = b\sin(kx - \omega t)$$



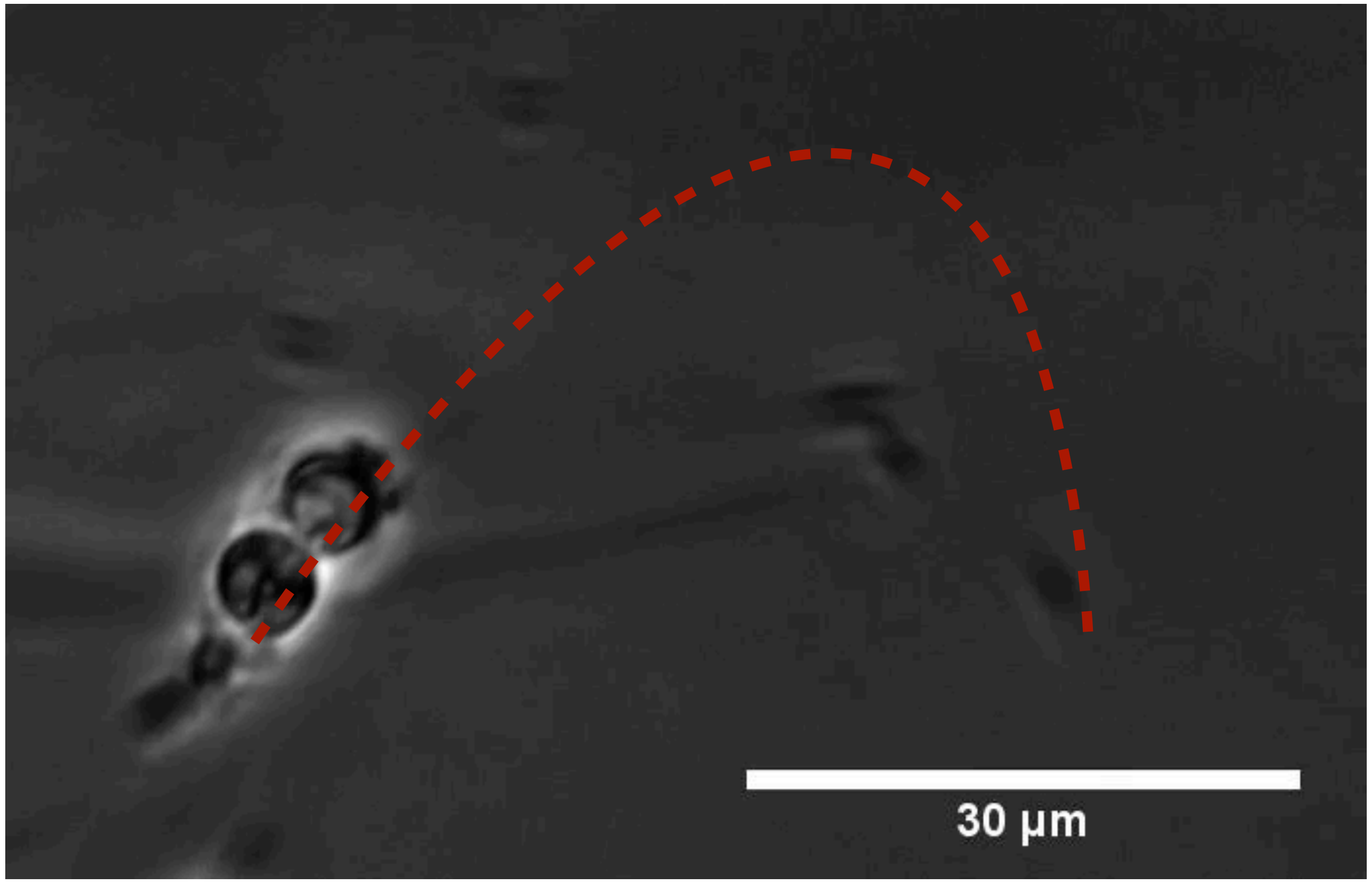
$$\mathrm{Er} = \frac{\mu U L}{K} = \tau\omega \qquad \theta_t + \overset{\nabla^{\perp}\psi}{\mathbf{u}} \cdot \theta = \frac{\mu}{\gamma\,\mathrm{Er}}\nabla^2\theta \qquad \nabla^4\psi + \frac{1}{2\mathrm{Er}}\nabla^4\theta = 0$$



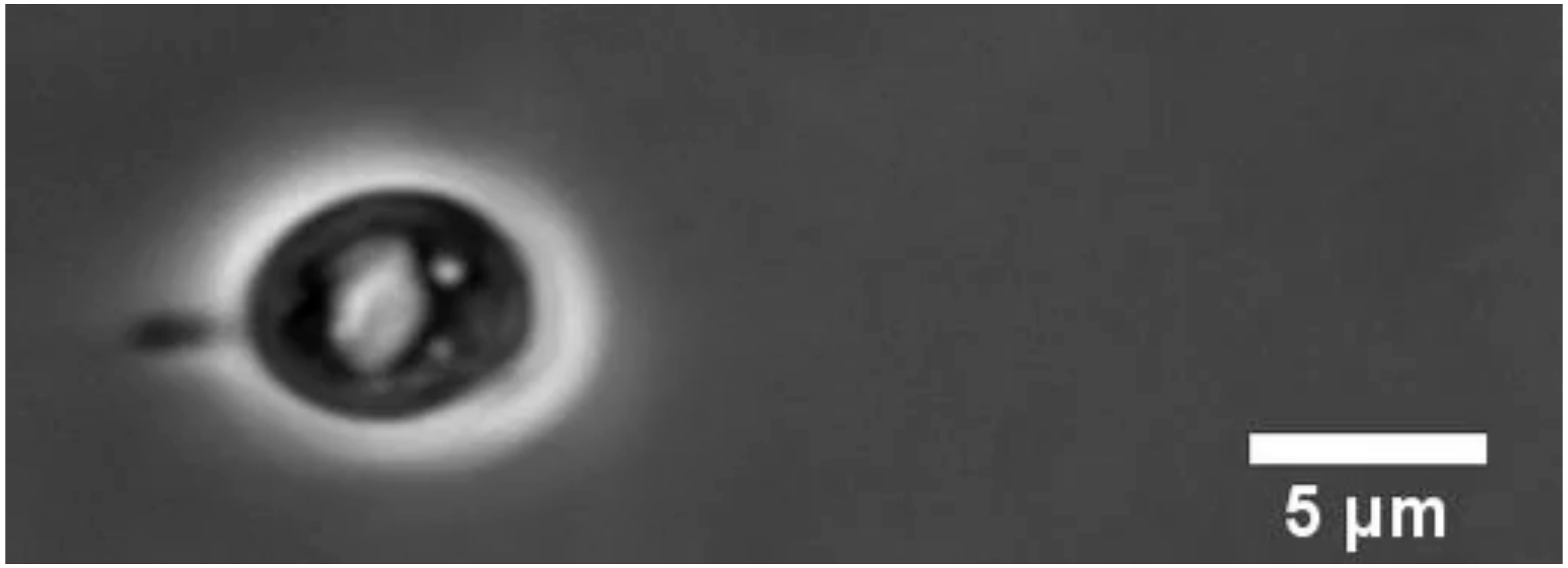


Krieger, Spagnolie & Powers, (2014, 2015, 2019)

Interesting new applications are just over the horizon…



Performing useful work?



Urinary tract infections?

. Trivedi, Maeda, Abbott, Spagnolie & Weibel, *Soft Matter*, 2015
. Mushenheim, Pendery, Weibel, Spagnolie & Abbott, *PNAS*, 2017

Main points I wanted to highlight:

Physical ideas:

1. Kinematic reversibility / Scallop theorem
2. Quasi-static dynamics
3. Drag anisotropy of slender bodies
4. Stochastic (e.g. run-and-tumble) trajectories
5. Inside the flagellum: flagellin/polymorphism, microtubules/axoneme

Mathematical tools:

1. "Stokeslet" fundamental solution (Green's function) and its derivatives
2. A boundary-integral representation*
3. Multipole expansion in the far-field: bacteria as force-dipoles.
4. Slender-body theory for thin filaments (flagella, cilia, etc.)

See also the following review articles:

Purcell, “**Life at Low Reynolds Number**”, Am. J. Phys. (1977)
Brennen & Winet, “**Fluid mechanics of propulsion by cilia and flagella**”, Annu. Rev. Fluid Mech. (1977)
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